

**Aspects of coral reef fish community structure
in the Saudi Arabian Red Sea and on the Great Barrier Reef.**

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DECLARATION

Some of the work presented in this thesis has been published previously. Chapter 5, 'Resource Sharing in Territorial Herbivorous Reef Fishes' was presented at the Fifth International Coral Reef Congress (Proc. Fifth Int. Coral Reef Congress, Tahiti 4: 17-22), and part of Appendix 2 has been published in Progress in Underwater Science (Vol. 11: 81-93). Dr Rupert Ormond is included as a co-author of Chapters 1 to 4; his contribution to these studies consisted of determination of many of the sampling procedures used and undertaking a few of the fish counts.

Errata

In Chapters 1, 3, and 5 the fish referred to as Plectroglyphidodon leucozonus is correctly known as Plectroglyphidodon leucozona

In Chapters 5 and 6 the fish referred to as Salarius fasciatus is correctly known as Salarias fasciatus, and in Chapter 6 Atrosalarius fuscus should be Atrosalarias fuscus.

It has recently been discovered that Chromis caerulea, referred to in Chapter 1, is a junior synonym of Chromis viridis.

ABSTRACT

The forces shaping fish community structure on coral reefs have been the focus of intense debate for over a decade. There have been two major theories put forward, one arguing that fish community structure has a deterministic basis, the other a stochastic basis. This study seeks to assess the importance of deterministic processes, primarily habitat selection, in structuring fish communities on the Saudi Arabian Red Sea coast. I also look at the mechanisms by which a group of species with very similar patterns of resource use coexist within the Red Sea and on the Great Barrier Reef. Fish communities have been studied at three scales: (1) geographic, (2) within-reef, and (3) within reef zones. At the largest scale, communities of damselfish, surgeonfish and parrotfish were found to differ markedly between regions of the Saudi Arabian coast (covering a distance of 1840km). These differences appear to be attributable primarily to differences in habitat between regions. Within reefs, damselfish were found to be broad-scale habitat specialists, most species only inhabiting one or two reef zones. Habitat differences between species were also apparent within reef zones. The extent of habitat differentiation between species was related to guild and seems to depend on the closeness of association species have with the substratum. Zonation patterns of damselfish over reefs were qualitatively consistent for most species between sites and between years (within sites) despite sometimes large differences in abundance of species, suggesting an underlying deterministic component to fish community structure. However, structural features of the substratum were found in most cases to be poor predictors of fish species richness and abundance indicating that habitat composition is not the only factor influencing fish community structure. At the within-zone scale, communities of territorial herbivorous fish which share space and food were studied in an attempt to discover how they are able to coexist without competitive exclusion. Size differences between species and behavioural adaptations appear to facilitate coexistence. However, the assumption that food or space (or both) are limiting may not always be valid. It is clear that any theory attempting to explain the structure of coral reef fish communities must include both deterministic and stochastic elements since these communities are neither completely ordered nor totally chaotic.

Introduction

INTRODUCTION*

Coral reefs have existed in one form or another for the last 450 million years and are restricted to the world's warm tropical seas. They cover vast areas of the shallow regions of these seas; for example, on the Great Barrier Reef the coral area covers approximately 20,300km² (Talbot, 1984). Bony fishes have inhabited coral reefs for around 400 million years and teleost fishes for approximately 200 million years (Romer, 1966).

Coral reefs support the most diverse fish assemblages of any aquatic habitat. These fish assemblages also constitute the most diverse vertebrate assemblages found anywhere in the world, aquatic or terrestrial. For example, One Tree Reef in the southern Great Barrier Reef, despite its small size (approximately 3-5km diameter), is known to be inhabited by over 860 species of fish (Russell, 1981). The reefs around Lizard Island in the northern Great Barrier Reef support over 1,000 species of fish (Talbot and Gilbert, 1981) and reefs in the Indo-Australian archipelago as a whole support well over 3,000 species (Goldman and Talbot, 1976).

The central aim of ecology is the understanding of patterns in the distribution and abundance of species (Krebs, 1972). Since the development of SCUBA diving around 40 years ago, coral reefs have become increasingly accessible to ecological research, and there has been a large expansion in such research since the 1960s. Fish communities have attracted a great deal of this research for several reasons. Many fish on coral reefs are highly conspicuous and can be approached relatively closely without apparently affecting their behaviour. This is in marked contrast to most terrestrial vertebrate communities. Additionally, most reef fishes are sedentary and have small home-ranges compared with terrestrial vertebrates (Sale, 1978a). The above characteristics make these communities very easy to observe and experimentally manipulate. Undoubtedly, the fact that fishes represent one of the most visually striking aspects of coral reefs has also contributed to the large amount of scientific interest shown in this group.

Early studies of coral reef fish communities were predominantly descriptive and drew heavily on theory developed from studies of terrestrial communities. Species were assumed to coexist through fine scale partitioning of resources, primarily space and food (Hiatt and Strasburg, 1960; Jones, 1968; Smith and Tyler, 1972). This resource

*References cited in this introduction can be found in the reference section following the overall discussion.

partitioning was assumed to be a consequence of interspecific competition for limiting resources, both past and present (Hutchinson, 1959; MacArthur, 1965; 1972; Pianka, 1966; Diamond, 1975). Tropical communities were thought to contain more species than those at higher latitudes for both historical and ecological reasons (Krebs, 1972). One of the major arguments put forward was that tropical species were able to become more specialised than those at higher latitudes because of the greater stability of the tropical environment, and thus a greater degree of species packing was possible (Pianka, 1966; MacArthur, 1969). The apparently benign and constant conditions prevailing in the shallow marine sublittoral of tropical regions would seem an ideal environment for such supposed niche differentiation in response to competition to become very pronounced. This view assumes that communities are usually at an equilibrium with stable individual species densities and overall composition (Doherty, 1983). Many studies, particularly from the Caribbean, have argued that coral reef fish communities are structured in this way (Smith and Tyler, 1972; 1973; 1975; Gladfelter and Gladfelter, 1978; Gladfelter et al., 1980; Gladfelter and Johnson, 1983; Robertson and Lassig, 1980; Waldner and Robertson, 1980; Anderson et al., 1981; Ogden and Ebersole, 1981). These studies have largely used a descriptive approach.

In the early 1970s, Peter Sale, working on a community of territorial, herbivorous damselfish, proposed an alternative theory to explain coexistence between fish species on coral reefs (Sale, 1974). This stemmed from the discovery that many of these species have apparently very similar patterns of resource use with little evidence of resource partitioning between them. Sale argued that coexistence between members of this guild was facilitated largely through stochastic processes. In a series of papers he developed this into what became known as the "lottery" hypothesis (Sale, 1975; 1976; 1977; 1978b; 1979; 1980; 1982; Sale and Dybdahl, 1975; 1978). Sale argued that the application of theory developed in studies of terrestrial animals to coral reef fish communities was inappropriate because of the very different life history characteristics of reef fishes (Sale, 1974). These life history characteristics are perhaps more similar to those of plants than to terrestrial animals. As already mentioned, post-larval fishes are relatively sedentary, typically having small home-ranges. With only one well-studied exception (Robertson, 1973) reef fishes have a larval dispersal phase (Sale, 1980). Fish either lay eggs on the substratum or spawn directly into the water column (broadcast spawners)(Thresher, 1984). In the former case the eggs are usually guarded by one parent until hatching, after which the larvae drift freely in the plankton for some period whilst they develop. This period varies from a few days to over one year (Brothers et al., 1983; Thresher, 1984; Doherty et al., 1985; Ogden, 1986). Losses during this planktonic dispersal phase are very high, and as a consequence, most reef fishes are prodigiously fecund (Thresher, 1982). Very large

numbers of eggs may be laid at a single spawning and many fish spawn daily throughout long breeding seasons (Thresher, 1984). It is not unusual for fish to lay more than 100,000 eggs, sometimes in single spawnings (Sale, 1980). It is generally held that whilst in the plankton, larval fishes are passively transported by currents since they are very weak swimmers (Sale, 1980; Williams et al., 1984). After some period of development within the plankton, larvae settle into suitable areas of coral reefs where they metamorphose into post-larval juveniles. These life history characteristics are critical elements of Sale's theory (Sale, 1974; 1978b).

Sale's lottery hypothesis suggests that coral reef fish communities are organised at the level of the guild rather than the species. One resource is suggested to limit the total density of species within each guild. Sale suggests that for most reef fishes this resource is space (Sale, 1978b). The major arguments of the lottery hypothesis in its original formulation are as follows:

1) That settlement of larvae from the plankton (hereafter termed recruitment) is only successful into areas of free space and that this space becomes available randomly, usually through the death of the former resident. Habitats are assumed to be at their carrying capacity.

2) That most species within a guild are able to occupy any given space and that which species does so depends on which species recruits into this space first. This depends on the assumption that most species are competitive equals and that prior residence at a site bestows a competitive advantage on the occupant over subsequent recruits.

3) The number of individuals of any species successfully recruiting to a reef is assumed to be unrelated to the abundance of the parental population.

4) Recruitment to a site is independent of the resident fish community.

Sale believes that high diversity in coral reef fish communities is maintained by this random recruitment of species into unpredictably available space (Sale, 1978b). Doherty (1983) refers to this as the multispecies equilibrium hypothesis because, whilst the densities of individual species are unstable, within guilds the overall density of species is stable.

The lottery hypothesis stimulated intense controversy amongst coral reef fish ecologists, dubbed the 'order and chaos' controversy (Bohnsack, 1983a; Ogden, 1986). However, it produced a series of testable predictions which stimulated equally intensive research and

triggered a change from the previously largely descriptive studies to experimental studies. In the following I shall briefly examine some of the current evidence concerning the predictions and assumptions of the lottery hypothesis.

1) Habitats are assumed to be at their carrying capacity Sale's initial studies on territorial, herbivorous damselfish suggested that all available space was occupied by these fish (Sale, 1974; 1975; 1979). Other studies on territorial herbivorous fish have also found high densities with little, if any, apparently habitable 'free' space (Williams, 1978; Robertson et al., 1979; Roberts, 1985). However, several studies involving density manipulations suggest otherwise. Robertson et al. (1981) concluded that space did not limit the densities of the Caribbean damselfish Stegastes planifrons and Doherty (1983) failed to find any density dependent mortality in another species of damselfish on patch reefs stocked at artificially high densities (although growth rates of some individuals were lower at high densities).

Amongst species with rather specific habitat requirements, such as anemonefish and the damselfish Dascyllus aruanus and D. reticulatus, which inhabit a few species of branched corals, space often appears not to be limiting either, considerable numbers of 'empty' and apparently habitable anemones and corals often being available (Fautin, 1986; Sweatman, 1983). Robertson and Sheldon (1979) showed that the availability of sleeping sites of the wrasse Thalassoma bifasciatum, which are defended, does not appear to limit the population density of this species. Evidence that food availability ever limits the populations of fishes other than those for which food and space are closely related (e.g. territorial herbivores) is very limited. Thresher (1983) showed that the abundance of the planktivorous damselfish Acanthochromis polyacanthus on patch reefs in One Tree Lagoon was inversely correlated with the numbers of individuals of other planktivorous species on those reefs, suggesting food limitation (or interference competition). Coates (1980) found that the largest (most dominant) individuals of the damselfish Dascyllus aruanus fed (on plankton) furthest upcurrent from the 'home' coral and were thus able to capture the largest prey. This suggests a limitation in the availability of such prey.

However, a number of other studies have found that the populations of fish on patch reefs are closely linked to levels of recruitment to those reefs, suggesting that population levels are set by recruitment rather than the carrying capacities of those reefs (Williams, 1980; Doherty, 1981; 1983; Victor, 1983; 1986). This expanding body of evidence implies that density limitation in coral reef fishes by density dependent processes is not as widespread as Sale originally believed (Sale, 1980).

2) The first recruit to settle at a site is able to hold it against subsequent recruits. There is very little evidence to test the validity of this assumption. In the only study I know of testing for priority effects in the recruitment of coral reef fish, Shulman *et al.* (1983) found that space on artificial patch reefs was not always appropriated on a first-come-first-served basis. Two kinds of priority effects were found. Settlement of juveniles of a species of predator lowered the recruitment success of two prey species, and one species of territorial damselfish significantly decreased recruitment success of three other species. There have been considerably more studies of freshwater fishes looking at the importance of prior residence on aggressive behaviour, although these have confined attention to adult fish, not to newly settling recruits (e.g. Figler and Einhorn, 1983; Bronstein, 1985). In these studies, prior residence at a site has frequently been found to bestow a competitive advantage on the residents over intruders (see Bronstein, 1985). However, these studies have limited attention to intraspecific interactions and so the interspecific effects of prior residence remain untested.

There are considerable difficulties with Sale's concept of 'free' space into which recruits may settle. Sale argues that free space is created usually by the death of the former resident (Sale, 1978b). However, whether such a model of juvenile establishment is realistic is debateable. If populations are not normally at the carrying capacity of the habitat, as some workers believe (Williams, 1980; Doherty, 1983; Victor, 1986), then clearly it is not. However, even where populations do exist at high densities, these densities may not affect recruitment or survival of juveniles (Doherty, 1983).

3) Recruitment is independent of the resident fish community. Sale's theory requires that the resident fish community has no differential effect on the success of recruits of different species to areas of available space. However, recent work has shown that recruitment is not always random with respect to species and that the presence of adults of some species may enhance recruitment of conspecific juveniles (Sweatman, 1985). This is a priority effect of a different kind and will tend to promote the formation of more deterministic fish assemblages.

4) Recruitment success is independent of adult stock. For high diversity to be maintained through stochastic recruitment, the cohort size of settling fish must be independent of the size of the adult breeding population for any given species. There is very little data on stock-recruit relations in fish (most is from fisheries studies) with which to test this assumption. Sale (1980) reviewed the available evidence and concluded that it did not falsify his assumption. Because of the pelagic larval dispersal phase, it is highly unlikely that fish recruiting to any area of reef will be the offspring of residents

(Sale, 1980; Williams et al., 1984; Doherty et al., 1985; Avise and Shapiro, 1986). This poses a major barrier to any studies of stock-recruit relations in coral reef fishes, since it is impossible to know with any accuracy the source of settling larvae. Most studies of recruitment have emphasised the enormous variability of the process in space and time, despite the regularity of spawning of many species (Talbot et al., 1978; Eckert, 1984; Sale, 1985) suggesting that independence of stock size and levels of recruitment is not an unrealistic assumption.

5) Most species within a guild are able to occupy any given space. One of the major lines of argument used against Sale's lottery hypothesis and given in support of more conventional competition based theories of community structure, is that many species show distinct habitat specialisation (e.g. Robertson and Lassig, 1980; Ross, 1986). There is now an increasing amount of evidence that, even within guilds, recruitment is not random with respect to habitat (Sale et al., 1984; Eckert, 1985). In more recent formulations of the lottery hypothesis Sale acknowledges this evidence for habitat specialisation but argues that it is of less importance in determining the structure of fish communities (at least on patch reefs) than variability in recruitment (Sale et al., 1984; Sale and Douglas, 1984).

Both resource partitioning-based theories of fish community structure and Sale's lottery hypothesis have been much criticised. Some workers now believe that coral reef fish communities are completely non-equilibrium, unstable at both the species and guild level. There are two main ways in which non-equilibrium conditions are thought to be maintained: environmental disturbance and recruit limitation (Connell, 1978; Doherty, 1983). The kind of disturbances most likely to affect reef fish communities are storms, and temperature and salinity fluctuations. A number of recent studies have shown the disruptive effects of tropical storms on fish assemblages (Beecher, 1973; Kaufman, 1983; Lassig, 1983; Walsh, 1983). Storms cause varying levels of direct mortality in fishes but their main effect is indirect through habitat destruction and modification (Walsh, 1983). This results in the redistribution of many fishes over the reef, primarily those resident in shallow water, and these patterns may remain stable for long periods following the storm (Kaufman, 1983; Walsh, 1983; Lassig, 1983). Lassig (1983) reports that the effects of storms are different between age-classes of fish. He believes that many juvenile fish, which are weak swimmers, are swept away and perish, whilst sub-adult fish are usually redistributed between areas of reef. Adult fishes were less affected in his study. Lassig argues that the frequency of tropical storms in many regions may prevent equilibrium conditions from ever becoming established. Other sources of density independent mortality, such as cold spells

(Bohnsack, 1983b) or lowered salinity due to freshwater runoff during storms, may have similar effects.

Sale originally believed that the availability of recruits of most fish species was virtually unlimited (Sale, 1978b). However, a number of studies indicate that the availability of recruits may limit population sizes of fish on patch reefs (Williams, 1980; Doherty, 1981; 1983; Victor, 1983; 1986; Sale, 1985). Doherty (1983) removed two species of territorial damselfish from a group of patch reefs and found that population levels had recovered to less than 50% of their original levels by two years later. Victor (1983) showed that populations of a short-lived wrasse, Thalassoma bifasciatum, on patch reefs directly reflected rates of recruitment to these reefs the year before, suggesting recruit limitation. Victor (1986) believes that recruit limitation in coral reef fishes is a general phenomenon and that by keeping populations at levels below those at which resources become limiting, it is the main mechanism by which large numbers of species are able to coexist on coral reefs. The generality of recruit limitation is, however, disputed (Sweatman, 1985).

The following studies investigate coral reef fish community structure in the Red Sea and on the Great Barrier Reef at both large and small scales. These studies are primarily concerned with understanding the factors which influence community structure and have specific relevance to the foregoing controversy in this field. I have studied communities at three scales: (1) geographic, (2) within-reef, and (3) within reef zones. The role of habitat type and microhabitat specialisation of species in determining fish community composition has been a major emphasis of these studies. At the geographic scale I have looked at the distribution and community composition of species of damselfish, surgeonfish and parrotfish on reefs along the Red Sea coast of Saudi Arabia. These studies are presented in Chapters 1 and 2. At the within-reef scale I have looked at vertical zonation patterns and their year-to-year variability in damselfish communities on Red Sea fringing reefs in order to assess how this reflects habitat specialisation and niche differentiation between species, factors important to the view that coexistence between species is facilitated by resource partitioning. The results of this are presented in Chapter 3. In the same study I also looked at the extent to which some species differ in their use of space resources within reef zones. In Chapter 4 I have studied the way in which habitat characteristics influence the richness and abundance of assemblages of species from five families of fish.

At the smallest scale I have attempted to define the factors which permit coexistence between a group of territorial herbivorous species which have apparently very similar resource requirements. These include surgeonfish, damselfish and blennies which live in close association in the shallow regions of coral reefs and feed primarily

on filamentous algae. Chapter 5 reports on a study of surgeonfish damselfish and blennies from fringing reefs in the Red Sea, and Chapter 6 on damselfish and blennies living in rubble habitats on the Great Barrier Reef.

As noted above, the majority of these studies were conducted on reefs on the Saudi Arabian Red Sea coast. Fieldwork was undertaken during three phases of two, three and three months respectively during the summers of 1982-1984. These field phases were part of a general survey of the distribution of coastal and marine habitats and species in Saudi Arabia being undertaken by the Tropical Marine Research Unit of the University of York. This survey involved visiting a large number of sites for, necessarily, short periods. This logistical basis imposed certain limitations on the studies reported here, the most important of which was that the studies are descriptive rather than experimental. It was not possible to stay at any site for long enough to perform experiments on the fish community and most sites could only be visited once. It is well known that carefully designed experiments are a more productive means of testing hypotheses than are descriptive studies, the results of which, at best, are poor at differentiating between competing hypotheses (Connell, 1974; Sale, 1984). Indeed, one of the major criticisms levelled at studies of resource partitioning is that they are usually only descriptive (Sale, 1984). However, I am fully aware of the interpretative difficulties inherent in descriptive studies and these are highlighted throughout.

Chapter 1

Biogeography of Red Sed Sea damselfish

(Pisces: Pomacentridae) on the Saudi Arabian coast.

ABSTRACT

There have been few studies which have described large-scale variation in the structure of coral reef fish communities. This study describes patterns in the community composition of damselfishes (Pomacentridae) and the distribution of species along the Red Sea coast of Saudi Arabia. Species present were recorded at sixty-one sites spanning around 1800km and 13° of latitude. At thirty-six of these sites counts of damselfish were made along a 100 x 5m transect laid at a depth of 1.5m on the reef-edge. Reef profiles were recorded at all sites in order to assess the relationship between community composition and gross reef structure. These data were analysed using numerical classification techniques. Much of the Saudi Arabian coast is bordered by fringing reefs but the structure of these alters dramatically at a point where the continental shelf widens. Central & northern regions are dominated by well-developed, deep clearwater reefs whilst southern regions are characterised by shallow, turbid reefs. This change has a marked effect on both the species composition and quantitative structure of damselfish communities. Contrary to expectations based on latitude and increasing isolation from the Indian Ocean source fauna, damselfish species richness did not decrease from south to north. Overall, twenty-seven, twenty-six and twenty-four species were observed in northern, central and southern regions respectively. However, numbers of species observed per site did not differ significantly between regions. The structural simplicity of reefs in the south and their lower areal coverage compared with reefs in central & northern regions probably account for the observed patterns.

INTRODUCTION

Coral reef fishes are characterised in almost all cases by the presence of a planktonic larval dispersal phase (Thresher, 1984). One probable consequence of this is that many species are distributed over very large areas (Scheltema, 1968). For this reason, most studies of fish biogeography have been conducted at very large scales; oceans rather than seas (e.g. Woodland, 1983; Thresher and Brothers, 1985; Springer, 1982). This study looks at the distribution of species at a smaller scale: within the Red Sea.

In contrast to studies of biogeography, there have been few studies which have looked at large scale variation in fish community structure and these have all covered distances much smaller than those dealt with in this study (Anderson et al., 1981; Williams, 1982; Williams and Hatcher, 1983, Russ, 1984a; b; but see Williams, 1983). We also investigate geographic variation in fish community structure in order to assess whether there is any systematic variation in community structure on reefs from north to south within the Red Sea.

Quantitative and qualitative measures of damselfish (Pomacentridae) community composition were made using visual census techniques at sites spread along the entire Saudi Arabian Red Sea coastline. Damselfish were chosen because they are abundant, ubiquitous and diverse on coral reefs (34 species in the Red Sea; Allen and Randall, 1980), and because they have been well studied in the past. In addition, measurements of gross reef morphology were made at the same sites to try to assess the possible contribution of reef morphology to damselfish community variation.

The Saudi Arabian Red Sea coastline is a particularly good location for such a study. It is around 1840km long and of this approximately 1640 km are bordered by more-or-less continuous fringing reef (Ormond et al., 1984). From north to south it covers 13° of latitude, allowing latitudinal influences on fish distribution to be studied.

This paper describes changes in the composition and structure of damselfish communities with latitude and habitat on the Saudi Arabian Red Sea coast. We investigate the importance of ecological factors in determining the distributions of component species of these communities and in maintaining differences in community structure between reefs in different regions of the Red Sea.

METHODS AND STUDY AREA

The study area.

The Red Sea is a long, narrow body of water which covers 18° of latitude in a NNW to SSE direction. It is enclosed between two desert landmasses and this leads to high rates of evaporative water loss with little compensatory precipitation. There are no permanent rivers flowing into the Red Sea. Hence, this evaporative water loss has gradually led to an increase in water salinity above that of the open Indian Ocean (Morcos, 1970). There is a net inflow of water from the Gulf of Aden through the shallow Straits of Bab el Mandab and this replenishes water lost through evaporation and it is primarily this which is the cause of a gradient of increasing salinity (37 p.p.t. increasing to 40 p.p.t.; Morcos, 1970) from south to north. There is also a gradient of decreasing surface temperature from south to north, average surface temperatures in July being around 31°C in the southern Red Sea compared with 25°C in the Gulf of Aqaba (Morcos, 1970).

Surface currents are variable and driven primarily by wind (Patzert, 1974; Mustafa et al., 1980). From October to April the winter monsoon causes the surface currents to flow NNW whilst from May to September their mean set is in the opposite direction (Patzert, 1974; Morley, 1975).

The geological history of the Red Sea is complex and has been described in more detail elsewhere (Price, 1982; Girdler, 1984; Johnson and Feltes, 1984; Winterbottom, 1985; Edwards, in press). In brief, the Red Sea began to develop approximately 25 million years ago (Davies, 1969). During the Miocene it was connected to the Mediterranean through the Gulf of Suez but had no connection with the Indian Ocean (Edwards, in press). In the early Pliocene the Red Sea became separated from the Mediterranean. At roughly the same time a connection became established with the Indian Ocean to the south. In the Pleistocene repeated glaciations caused global sea levels to rise and fall several times. It is thought that this resulted in isolation of the Red Sea, perhaps several times, as water levels fell below the shallow sill in the Straits of Bab el Mandab, although this is disputed. This may have led to complete evaporation of the Red Sea and consequent extinction of its fauna (Klausewitz, 1972; Price, 1982). Hence, species now present in the Red Sea may all have colonised since the last glaciation (ca 10,000 years B.P.)(Winterbottom, 1985).

The Saudi Arabian coast is bordered along most of its length by fringing reefs. Red Sea fringing reefs are well-known for their characteristic structure. Typically, there is a reef-flat or shallow lagoon of variable width extending to close to the seaward margin of the reef. At the reef margin there is a well-defined reef-edge at which there is usually a very abrupt drop-off into deep, clear water (Mergner, 1971; Loya, 1972; Vine and Vine, 1980). However, during this

survey it was found that this structure is typical of reefs only from the central & northern regions of the Saudi Arabian coast. In the southern region reefs are generally less well-developed and are found in shallow, turbid water (Ormond et al., 1986). This change in reef structure occurs over only approximately 60km of coast (referred to hereafter as the 'habitat discontinuity'), over an area corresponding to the point where the width of the continental shelf increases (going from north to south). Because reef structure changes over such a short distance it is possible to distinguish between habitat-related differences in damselfish communities and latitudinal effects.

Data collection

Species presence/absence The damselfish species present at 61 sites along the Saudi Arabian coast (Figure 1) were recorded during a thirty minute swim at each site using snorkelling gear, and, at deep reefs, on an additional 20 minute dive using SCUBA. All reef zones were examined during the census period. Damselfish species found in the Red Sea are all diurnal and most are conspicuous. However, particular attention was given to searching for secretive or uncommon species. During the swim a length of approximately 200m of reef was surveyed. To assess whether this was sufficient to adequately sample most of the species present at a site, cumulative species-area curves were determined for two sites in the central Red Sea, Jeddah and Shu'aiba. Damselfish were censused in vertical, adjacent, 5m wide (visually estimated) transects extending from the reef-edge to a depth of 16m using SCUBA. On the first transect all species seen were recorded, on the second all those seen not present on the first were recorded, and so on. Fifteen transects (75m long section of reef) were censused at each site.

In other disciplines, such as coral community biology, minimum sampling area is usually taken as the area sampled after which doubling of the area yields an increase in the number of species recorded of 10% or fewer (Wienberg, 1981). At Shu'aiba, an asymptote in the number of species recorded (18) was reached after five vertical transects had been censused, a linear distance along the reef of 25m (375m^2)(Figure 2). By the above criterion, the minimum sampling area was four transects, doubling the number censused to eight giving only a 6% increase in the number of species observed. At the Jeddah site, new species were still being encountered up to transect fourteen, a linear distance of 70m (1050m^2)(Figure 2). The gradient of the fitted line on the log-log plot gives an increase of approximately 25% in the number of species for each doubling in sampling area, and thus minimum area cannot be determined for the Jeddah site. However, it is likely that an asymptote in the number of species recorded has nearly been attained. Hence, by sampling a 200m section of reef most of the damselfish species present at a site will be recorded.

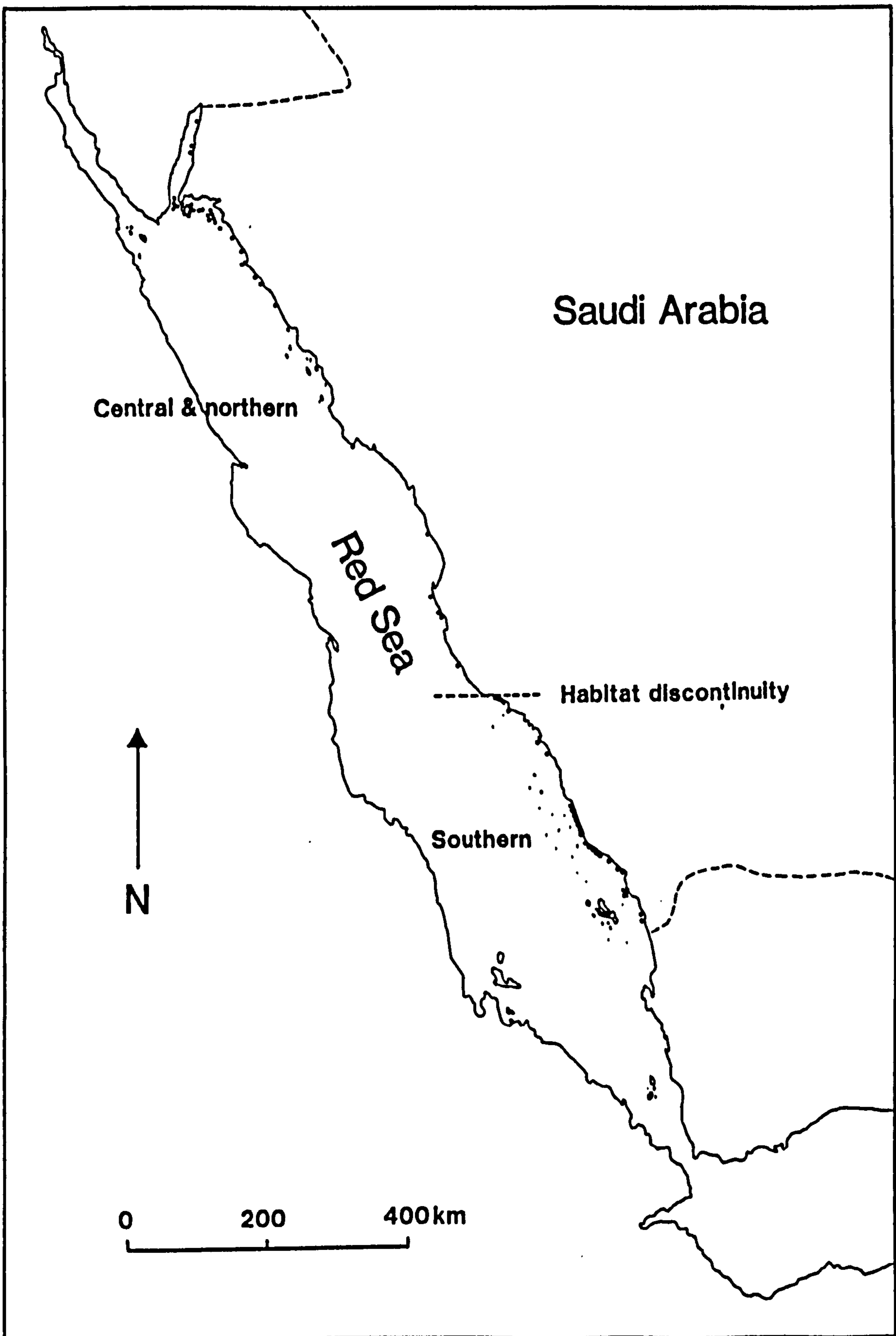


Figure 1: Map of Saudi Arabia showing the locations of study sites. The division between central & northern and southern regions used in this study is based on the location of the habitat discontinuity where, moving from north to south, deep, clearwater reefs are replaced by shallow, turbid reefs.

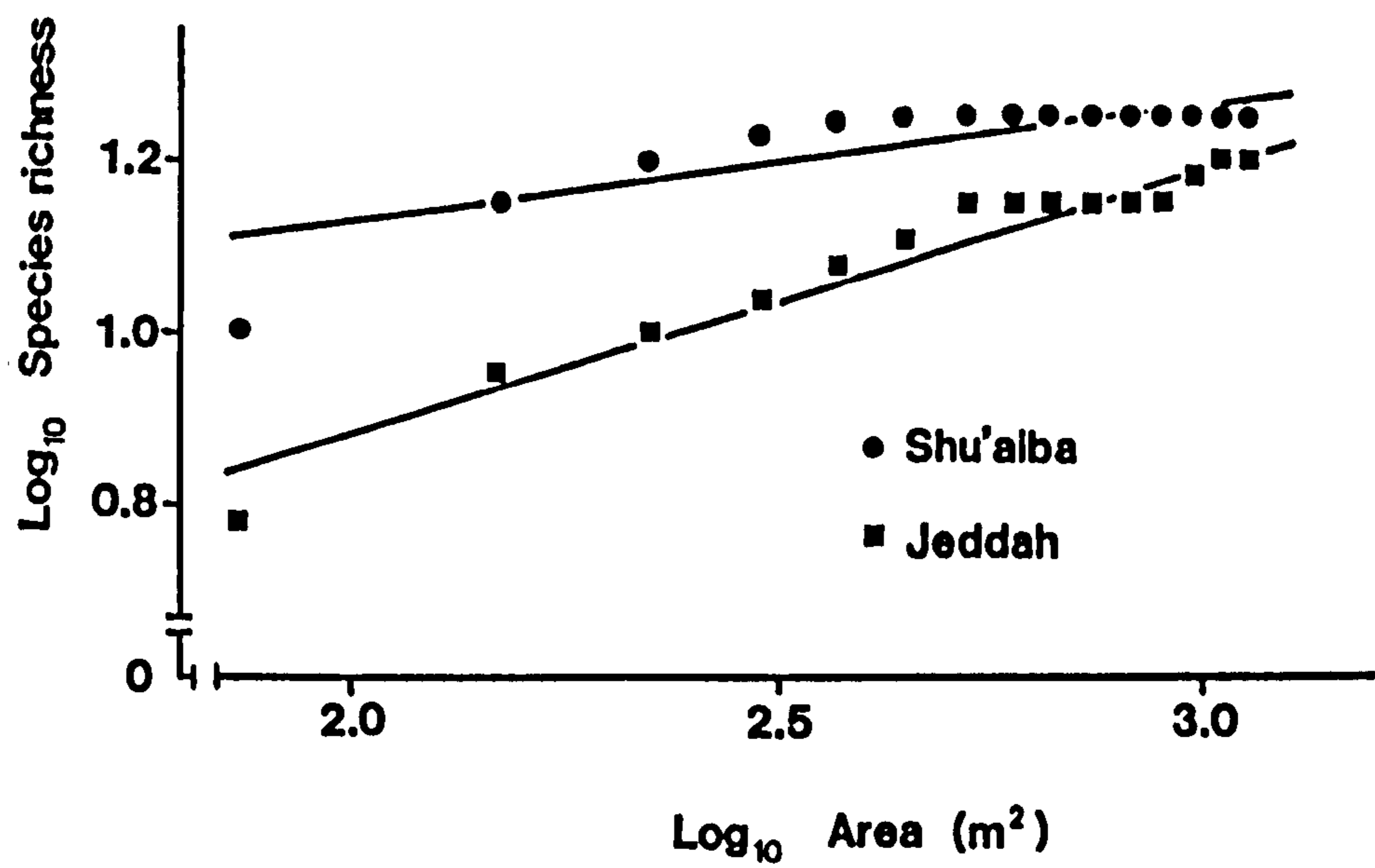


Figure 2: Species-area plots for damselfish from two sites in the central Red Sea. Lines were fitted using linear-regression.

Sampling intensity was not completely even between sites and those sites visited for longer periods will have more complete species lists than those at which only the above censusing method was employed.

A considerable number of island reefs in the northern Red Sea were censused during this survey. Unfortunately it was not possible to visit islands and reefs of the Farasan Bank and Archipelago in the south. However, a large number of underwater photographs were taken during a prior survey of this area (Ormond et al., 1986). These photographs were analysed for the presence of damselfish species allowing a more complete record to be made of species distributions within the southern Red Sea.

Using the above data the distributions of each species along the Saudi Arabian coast were mapped. In addition, cluster analyses (Ward's error sum of squares method, Wishart 1978) were run on these data in order to investigate the variation in species composition of damselfish communities throughout the study area.

Species abundance At 36 of the 61 sites visited, the numbers of individuals were counted of each damselfish species present within a 100 x 5m transect laid at a depth of approximately 1.5m along the reef-edge. This depth was chosen because (1) on Red Sea reefs it is the depth at which damselfish are most abundant (Roberts and Ormond, in prep. b), (2) the reef-edge is usually clearly defined, and (3) at this depth counts could be made whilst snorkelling which minimises the disturbance to resident fish (Roberts, 1986). The transect width was visually estimated as 2.5m either side of a 100m leaded rope. These data were analysed using Ward's error sum of squares clustering procedure as above.

Reef structure A profile of each site visited was sketched in order to determine whether there was any relationship between the damselfish community present on a reef and the gross structure of the reef. A cluster analysis was performed as above using six measures of reef morphology: (1) number of definable reef zones, (2) width of Sargassum belt at reef crest, (3) width of hard coral dominated area, (4) angle of reef-face, (5) angle of fore-reef slope, and (6) depth at the base of the fore-reef slope.

RESULTS

Distribution of species

In the following the patterns of distribution of species along the Saudi Arabian coast are described in a sequence corresponding to their overall geographic ranges. These ranges are broadly categorised as (1) endemic, (2) western Indian Ocean, and (3) Indian Ocean, Indo-Pacific and circumtropical (Figure 3).

Of the 34 species of damselfish known from the Red Sea, eight (23%) are endemic (Table 1), and the ranges of four of these extend into the Gulf of Aden (Allen and Randall, 1980). Figure 3 shows the distributions of these species along the Saudi Arabian coastline. Three of these species, Neopomacentrus xanthurus, Amblyglyphidodon flavilatus and Amphiprion bicinctus, occur along most of the Saudi coast; the planktivores N. xanthurus and A. flavilatus become much more common towards the south, appearing to favour the shallow, silty habitats which predominate there. The anemonefish A. bicinctus is nowhere abundant but occurs at similar densities throughout its range.

Five of the endemic species are found over only restricted regions of the Saudi coast. Pristotis cyanostigma was, with one exception, only observed on reefs over a small stretch of coastline in the southern Red Sea. The exception was a silty reef located within a bay, in the northern Red Sea. It is likely that this species will be found on silty reefs in bays and mersas throughout the length of the Saudi coast, but only a few such sites were studied.

Chromis trialepha and Neopomacentrus miryae are found on the deep, clear reefs of the central & northern Red Sea. N. miryae becomes increasingly abundant with increasing latitude. Whilst it is found in only small numbers on reefs near Jeddah, it is probably the commonest damselfish in the Gulf of Aqaba (Dor and Allen, 1977). C. trialepha was only observed on fringing reefs as far south as Shu'aiba, but photographic evidence confirms its presence on deep, island reefs further south (Figure 3). The range of Pomacentrus leptus extends into the central Red Sea but it is most common on reefs in the south. Pomacentrus albicaudatus is restricted to the southern Red Sea.

Seven species found in the Red Sea occur throughout part or all of the western Indian Ocean. Pomacentrus sulfureus occurs in similar densities throughout the length of the Saudi coast. In contrast, Pomacentrus trilineatus is much more common in the south than in the north. Primarily a lagoonal species in the central & northern Red Sea, it undergoes a habitat shift with decreasing latitude, being found in the fore-reef zone of southern Red Sea reefs. Pomacentrus trichourus is found only in the central & northern Red Sea and becomes more common towards the Gulf of Aqaba. It is found on both silty and clearwater reefs throughout its Red Sea range.

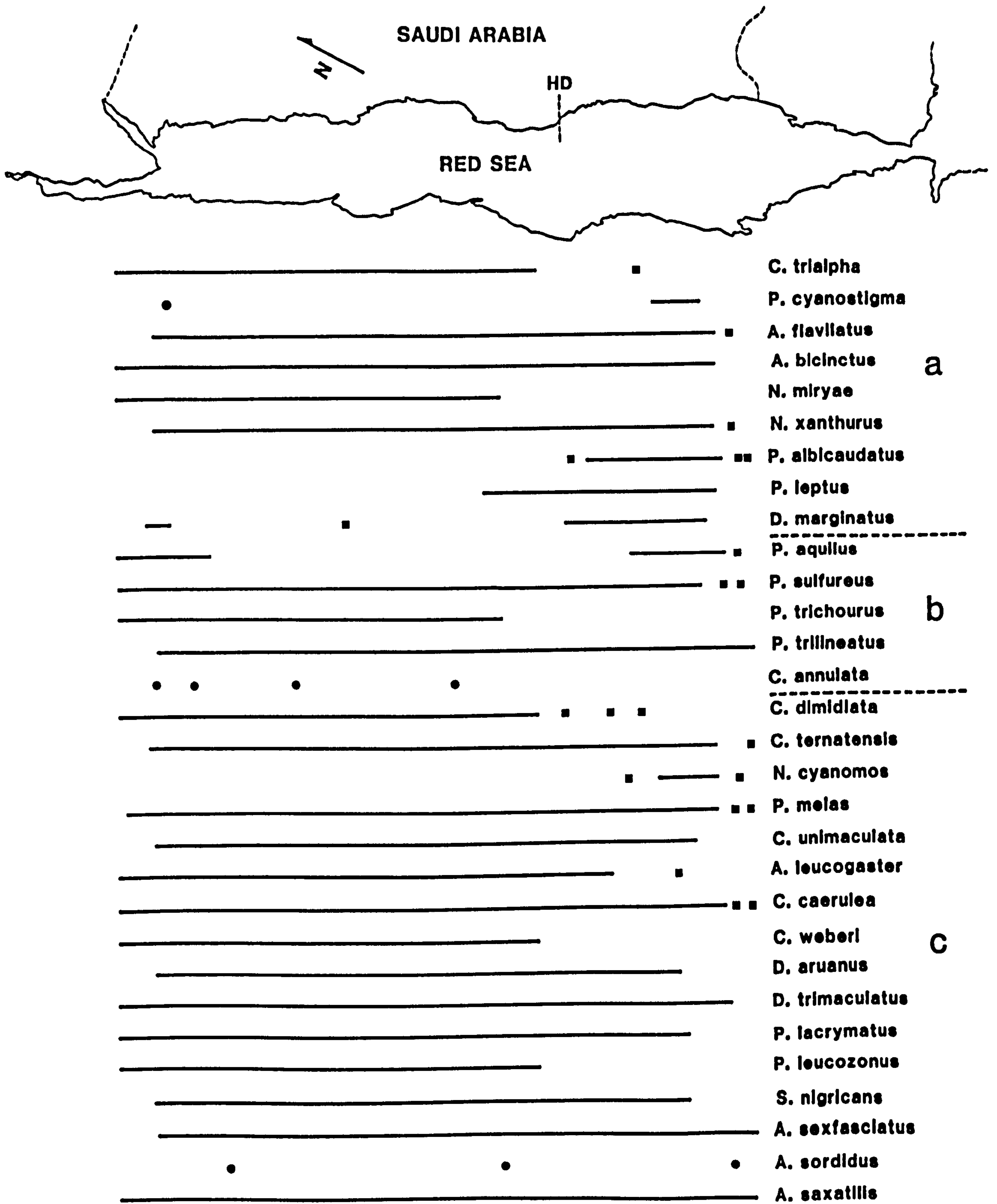


Figure 3: Distributions of damselfish species along the Saudi Arabian Red Sea coast. Circles show the sites at which species were observed for those species which were only recorded from a small number of sites. Squares represent photographic records of species, primarily from offshore and island reefs in the southern Red Sea. (a) = endemic species, (b) = western Indian Ocean species, and (c) = Indian Ocean, Indo-Pacific and circumtropically distributed species. 'HD' marks the location of the habitat discontinuity on the Saudi Arabian coast.

<u>SPECIES</u>	<u>DISTRIBUTION*</u>	<u>FOOD HABITS**</u>	<u>REFERENCES</u>
<u>Abudefduf saxatilis</u>	circumtropical	O	1,2,3,4
<u>A. sexfasciatus</u>	Indo-Pacific	O	3,4,5
<u>A. sordidus</u>	Indo-Pacific	O	2,3,4,6,7
<u>Amblyglyphidodon flavilatus</u>	Red Sea & G of A	P	pers. obs.
<u>A. leucogaster</u>	Indo-Pacific	P	4
<u>Amphiprion bicinctus</u>	Red Sea & G of A	O	3,4
<u>Chromis caerulea</u>	Indo-Pacific	P	2,4
<u>C. dimidiata</u>	Indian Ocean	P	4
<u>C. pembae</u>	W. Indian Ocean	P	3,7
<u>C. ternatensis</u>	Indo-Pacific	P	3
<u>C. trialpha</u>	Red Sea	P	pers. obs.
<u>C. weberi</u>	Indo-Pacific	P	3
<u>Chrysiptera annulata</u>	W. Indian Ocean	H	3, pers. obs.
<u>C. unimaculata</u>	Indo-Pacific	H	2,3
<u>Dascyllus aruanus</u>	Indo-Pacific	O	2,3,4
<u>D. marginatus</u>	Red Sea to G of O	O	3,4
<u>D. trimaculatus</u>	Indo-Pacific	O	3,4,7
<u>Neopomacentrus cyanomos</u>	Indo-Pacific	P	pers. obs.
<u>N. miryae</u>	Red Sea	P	3,4,8
<u>N. xanthurus</u>	Red Sea & G of A	P	pers. obs.
<u>Paraglyphidodon melas</u>	Indo-Pacific	O	3,7,10
<u>Plectroglyphidodon lacrymatus</u>	Indo-Pacific	H	2,4
<u>P. leucozonus</u>	Indo-Pacific	H	pers. obs.
<u>Pomacentrus albicaudatus</u>	Red Sea	O	pers. obs.
<u>P. aquilus</u>	W. Indian Ocean	H	3,4
<u>P. leptus</u>	Red Sea	O	pers. obs.
<u>P. sulfureus</u>	W. Indian Ocean	O	4, pers. obs.
<u>P. trichourus</u>	W. Indian Ocean	O	3,4
<u>P. trilineatus</u>	W. Indian Ocean	H	pers. obs.
<u>Pristotis cyanostigma</u>	Red Sea & G of A	P	pers. obs.
<u>Stegastes nigricans</u>	Indo-Pacific	H	2,9

Table 1: Damselfish species observed during this study. * Distributional ranges are those given in Randall (1983).** 'H' = herbivore, 'O' = omnivore, and 'P' = planktivore. References are: (1) Randall (1968), (2) Hiatt and Strasburg (1960), (3) Fricke (1977), (4) Fishelson et al. (1974), (5) Fishelson (1977), (6) Hobson (1974), (7) Allen and Randall (1980), (8) Dor and Allen (1977), (9) Allen (1975), and (10) Randall (1983). G of A = Gulf of Aden, and G of O = Gulf of Oman.

Pomacentrus aquilus has a discontinuous distribution, the northern Red Sea population being isolated from the southern by around 1000km. Its apparent absence from this region cannot be attributed to sampling inefficiency since it is a conspicuous territorial herbivore which inhabits the shallow areas of the fore-reef (reef-flat and 1m terrace zones) and these were thoroughly censused.

Dascyllus marginatus lives in sandy areas sheltering among branches of coral, usually of the genus Stylophora. It is an uncommon species but may be locally abundant. D. marginatus was not observed over a large central section of the Saudi Arabian coast but is likely to be present in the silty habitats of bays and mersas in this region. Chrysiptera annulata likewise occupies sandy, lagoonal habitats and is uncommon. It was only observed at a few sites from the central to the northern Red Sea. Again, this is probably due to a less intensive sampling of lagoonal habitats than other reef zones.

Chromis pembae is a schooling planktivorous fish which inhabits the deep areas of the fore-reef slope (usually below 20m). It was only observed at two sites, Jeddah and Shu'aiba in the central Red Sea, probably because few deep observations (20m+) were made on reefs elsewhere. Randall and Swerdloff (1973) and Fricke (1977) record it from the Gulf of Aqaba but it is absent from fringing reefs of the southern Red Sea (although it is possibly present on the reefs of some offshore islands).

The remaining sixteen species in this study have larger geographic ranges, occurring throughout the Indian Ocean, Indo-Pacific or circumtropically. Only five of these are not found over the majority of the Saudi Arabian coastline. Chromis dimidiata is the most abundant and ubiquitous damselfish in the central & northern Red Sea but is completely absent from fringing reefs south of the habitat discontinuity. Photographic records indicate that it is present on some island reefs further south but apparently is absent from the Farasan Islands. Chromis weberi and Plectroglyphidodon leucozonus are also found on fringing reefs only in the central & northern Red Sea. C. weberi is usually most common in the deeper regions of the fore-reef (> 15 - 20m), whilst Pl. leucozonus is a territorial herbivore which is abundant in the 1m terrace/reef-flat zone but is never found below a depth of approximately 3m. The distribution of Amblyglyphidodon leucogaster extends further south than C. weberi or Pl. leucozonus but it becomes very uncommon south of the habitat discontinuity. In contrast, Neopomacentrus cyanomos is only found on fringing reefs of the most southerly part of the Saudi coast.

Chromis ternatensis, C. caerulea, Abudefduf sexfasciatus, A. saxatilis and Plectroglyphidodon lacrymatus are common over most of the length of the Red Sea, whilst Stegastes nigricans and Dascyllus aruanus are more patchily distributed but may be locally abundant throughout this area. Chrysiptera unimaculata becomes less common with decreasing latitude. Similarly, Dascyllus trimaculatus is less common

in the southern than in the central & northern Red Sea. Paraglyphidodon melas is present in low numbers throughout the survey area but is most common in the Gulf of Aqaba. Abudefduf sordidus was only observed at three, well separated, sites on the Saudi coast but this probably reflects the fact that it is usually found in rocky or lagoonal habitats (less well surveyed in this study than other habitats) and because it is a timid species, rather than because it was absent from the intervening areas.

Reef Structure

Figure 4 shows the classification of reefs obtained using Ward's error sum of squares clustering procedure (Wishart, 1978) with six measures of gross reef morphology. Taking a Euclidean distance of 6.00 as the level at which clusters are distinguished, six clusters are defined (Figure 4). The average structures of reefs from each cluster are shown in Figure 5.

Cluster 1 These reefs are found in the northern Red Sea and drop steeply into clear water (Figure 5). They lack a lagoon, Sargassum zone (a band of Sargassum algae along the reef crest) and lm terrace zone, these zones being replaced by a, usually narrow, reef-flat.

Cluster 2 Reefs from cluster 2 are similar to those in cluster 1 (Figure 5) but are better differentiated into zones in the shallow regions, having clearly defined lagoon, Sargassum and lm terrace zones. They drop steeply into clear water and the fore-reef slope zone usually grades into a steep sand slope at a depth of 35 - 40m. Such reefs are found throughout the central Red Sea.

Cluster 3 Reefs from cluster 3 are found in the northern Red Sea. This structure is represented in both mainland and island fringing reefs, and offshore patch reefs. They typically have a broad reef-flat and drop steeply to a sand sea-bed at a depth of 10 - 20m (Figure 5). This sand bottom is sometimes dotted with small patch reefs. Again, there is no lagoon, Sargassum zone or lm terrace.

Cluster 4 These reefs are similar in structure to cluster 3 but usually have a narrow reef-flat and Sargassum zone and drop steeply to a sand bottom at 4 - 8m deep (Figure 5), thus lacking a fore-reef slope zone. They are found throughout the Red Sea, often in turbid environments such as bays and mersas. The region of live, hard coral dominance on these reefs is typically very narrow.

Cluster 5 Reefs of this structure are found only in the southern Red Sea. They are characterised by a narrow reef-flat and a broad, dense Sargassum zone which grades into a gently sloping fore-reef, dropping

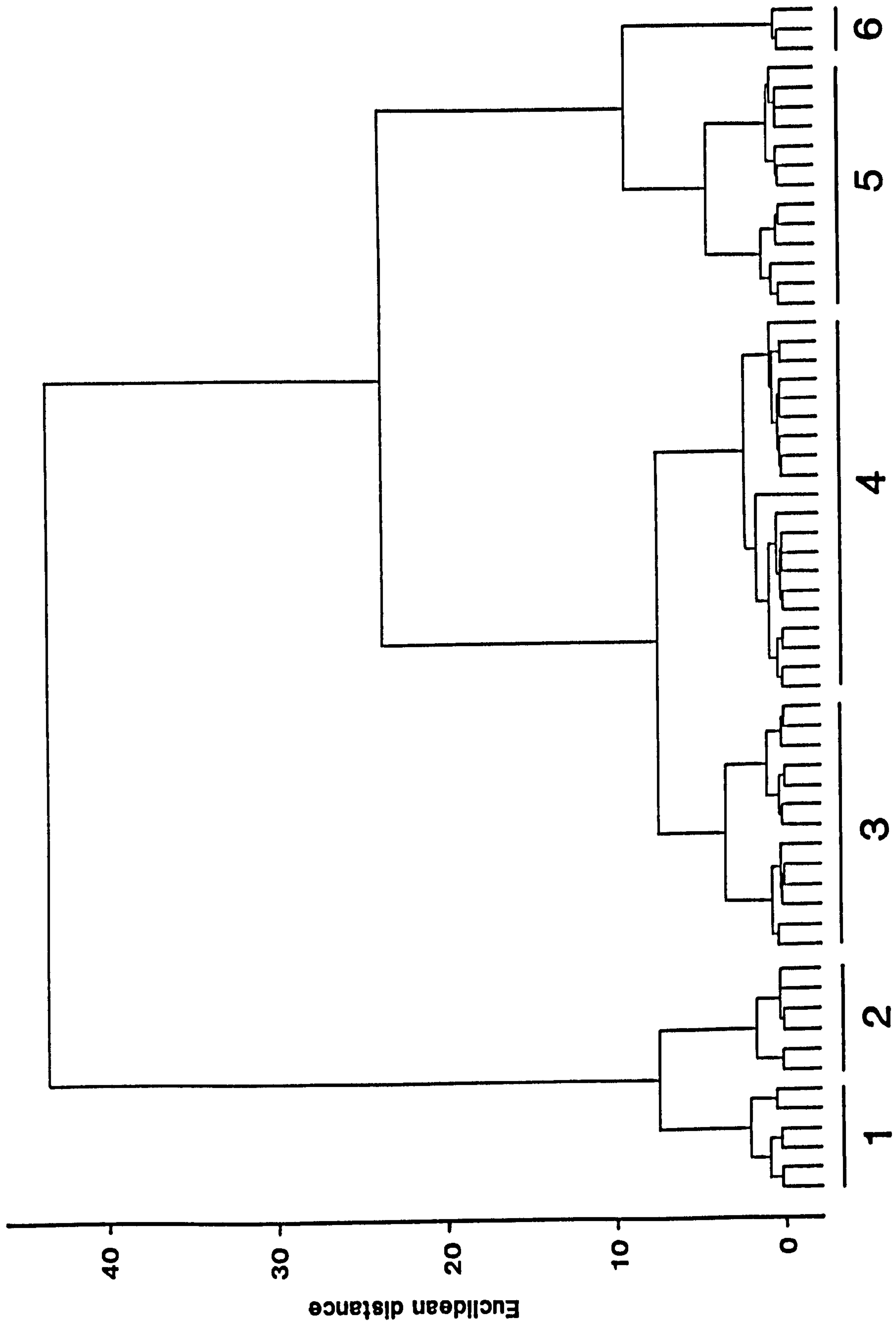


Figure 4: Classification of sites based on reef structure, using Ward's error sum of squares method. Six clusters are defined at a Euclidean distance 6.00. The average structures of reefs from each cluster are shown in Figure 5.

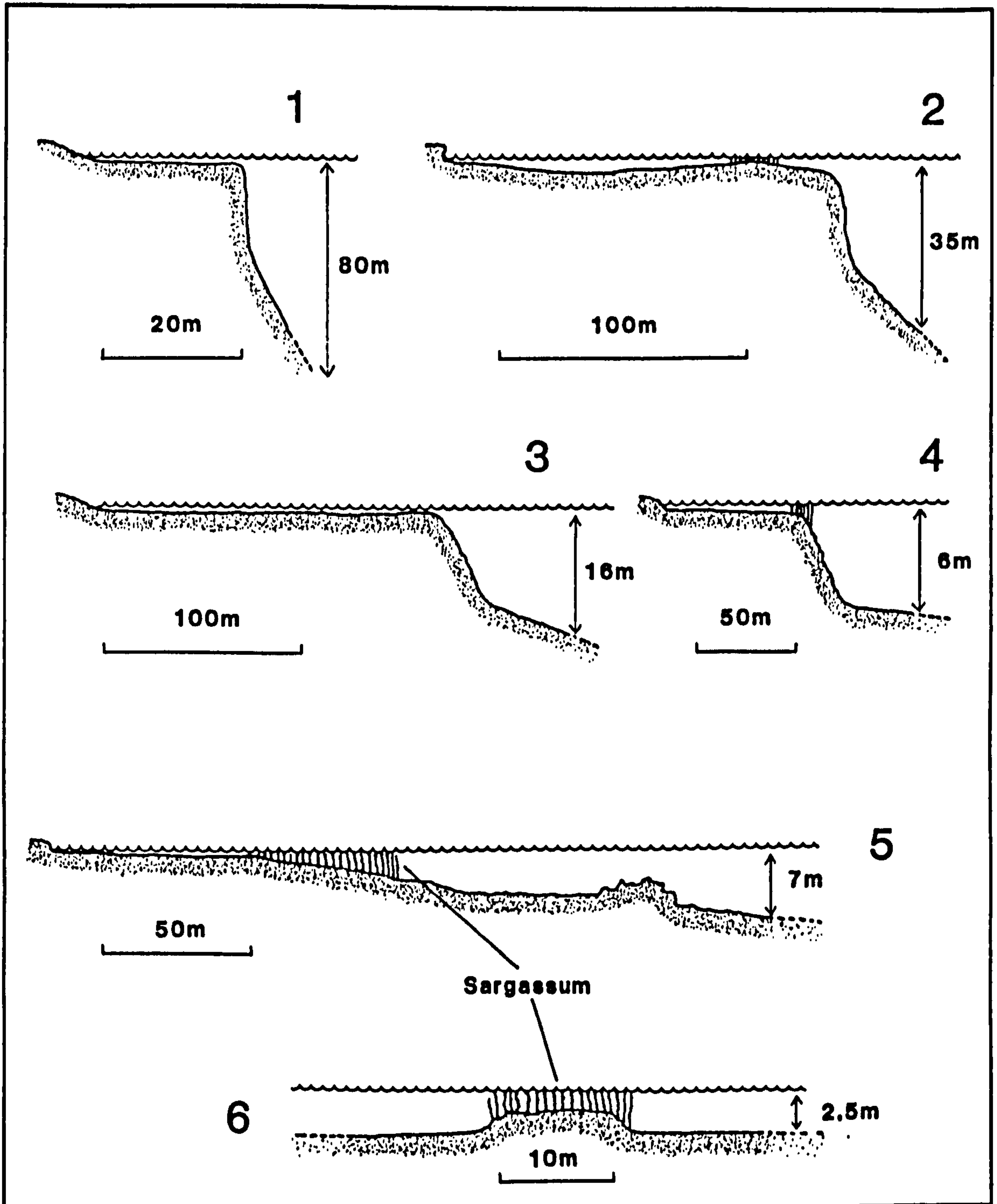


Figure 5: The average structures of reefs from the six clusters defined in the reef structure analysis (Figure 4).

to a sand bottom at a depth of 4 - 6m (Figure 5). This fore-reef slope is dominated in its upper regions by turf-forming filamentous algae and in its lower regions by hard corals.

Cluster 6 Cluster 6 is comprised of only three sites, all from the far southern Red Sea. These reefs are all patch reefs composed primarily of coralline algae with a very low coverage of live, hard corals. They lie in 1 - 3m of very turbid water in sandy areas and are covered with dense growths of Sargassum (Figure 5).

Damsel fish community structure

Species composition Four clusters are defined at a Euclidean distance of 1.50 on a classification of species presence/absence data from each site (Figure 6). Cluster A includes sites only from the northern Red Sea, cluster B sites in both the central and northern Red Sea, and clusters C and D from the southern Red Sea (with two exceptions in cluster C).

The species composition of damselfish communities from the central & northern Red Sea (clusters A and B) is very different from that of communities found in the southern Red Sea (south of the habitat discontinuity, Figure 1; clusters C and D).

Figure 6 shows the correspondence between the classification of sites based on reef structure and this analysis based on damselfish presence/absence. Similarities between these classifications suggest that some of the differences in damselfish community composition between regions of the Red Sea are related to between-region differences in reef structure. For example, cluster 5 from the reef structure analysis and cluster D from the damselfish community analysis have very similar memberships. Similarly, cluster C from the fish analysis is composed almost entirely of algal reef (cluster 6) and shallow, turbid reef sites (cluster 2). Alternatively, these similarities may arise through damselfish community composition and reef structure covarying under the influence of some other undefined factor(s). Correspondence between reef structure and resident damselfish community composition in the central & northern Red Sea is much less marked (Figure 6).

Quantitative data Figure 7 shows the results of the cluster analysis based on counts of damselfish along a 100 x 5m transect laid at a depth of 1.5m on the fore-reef at each of 36 sites (data standardised to prevent results being biased by species with large variances in abundance; Wishart, 1978). Taking a Euclidean distance of 6.00 as the level at which clusters are distinguished, two clusters are defined (Figure 7). Cluster 1 consists entirely of sites from the central & northern Red Sea whilst cluster 2 is composed of sites from the southern Red Sea, with one exception, a turbid, shallow reef from

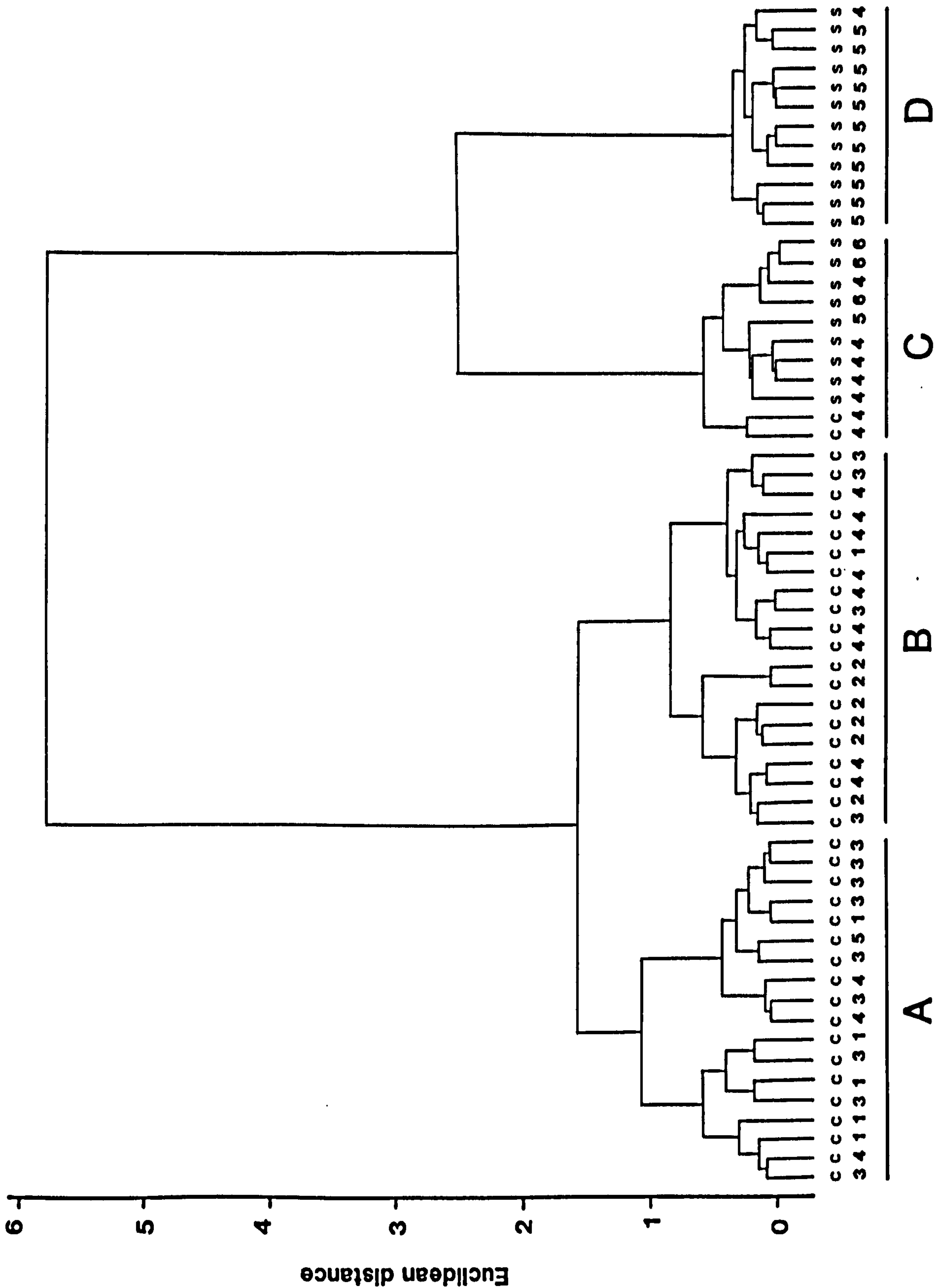


Figure 6: Classification of sites based on damselfish species presence/absence data, using Ward's error sum of squares method. Four clusters are defined at a Euclidean distance of 1.50. Sites marked 'C' are from the central & northern Red Sea and 'S' from the southern Red Sea. Numbers 1-6 correspond to cluster membership of sites as defined in the reef structure analysis (Figure 4).

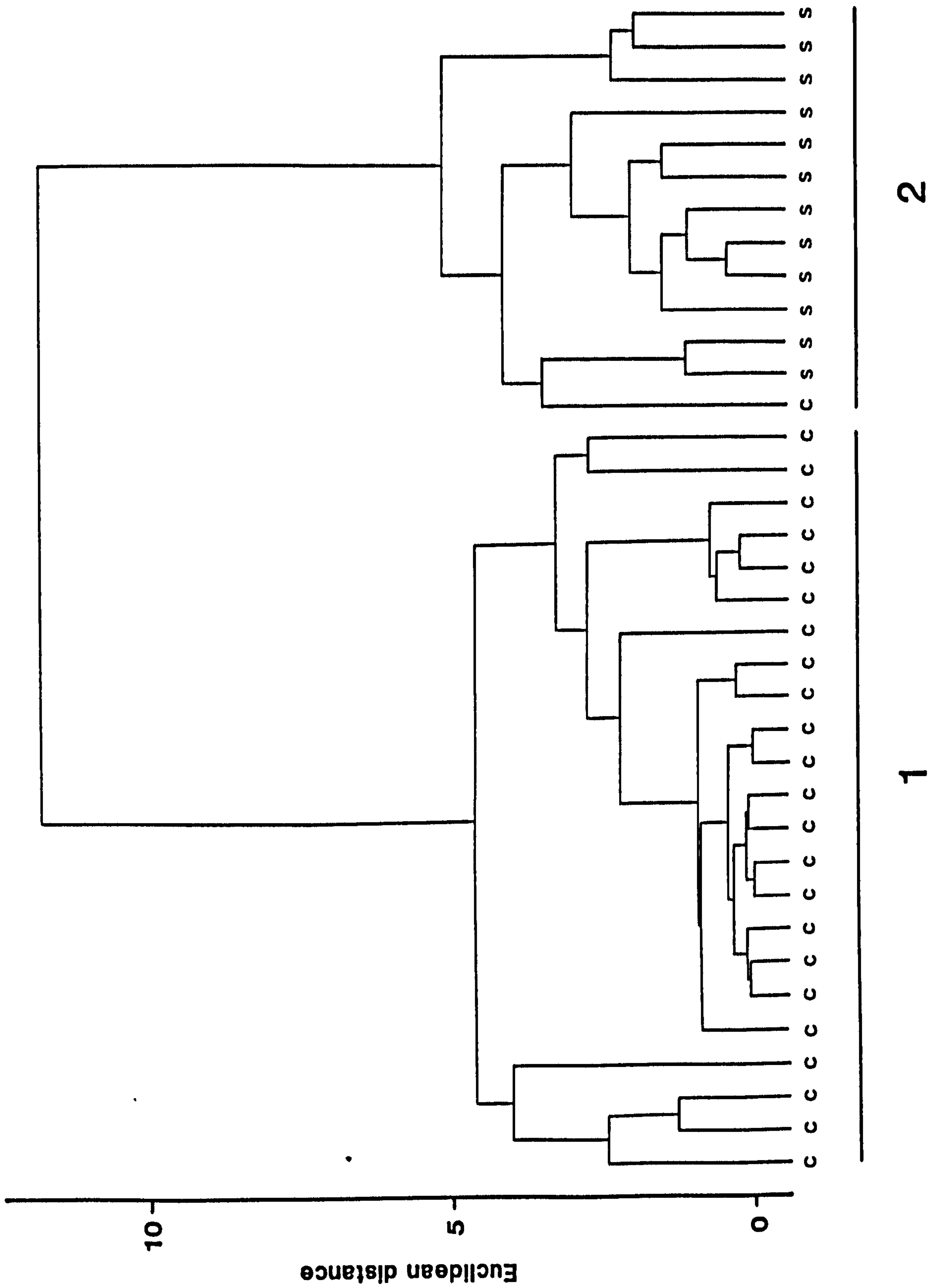


Figure 7: Classification of sites based on counts of damselfish along 100 x 5m transects, using Ward's error sum of squares method. Two clusters are defined at a Euclidean distance of 6.00. Sites marked 'C' are from the central & northern Red Sea and 'S' from the southern Red Sea.

the northern Red Sea. This indicates that damselfish communities from reefs to the north and south of the habitat discontinuity are distinct not only in terms of species composition but also in quantitative structure.

Patterns of species richness

Taking the habitat discontinuity (Figure 1) as the division between central & northern and southern regions of the Red Sea, sites in the central & northern region had an average of 12.0 ± 4.4 (S.D.) damselfish species ($n = 40$) compared with 11.7 ± 5.8 (S.D.) in the southern Red Sea ($n = 21$). There is no significant difference in within-site species richness between these regions of the Red Sea (Mann-Whitney U-test, $P > 0.10$). However, dividing the Saudi Arabian coast into three approximately equal areas (northern, central and southern), there were respectively 27, 26 and 22 species of damselfish observed in each region (24 species in the south if photographic records of species from offshore and island reefs are included). The central and northern regions of the Red Sea thus have a slightly higher between-habitat component to diversity than the southern Red Sea.

DISCUSSION

Distribution patterns

Latitudinal effects Where changes in the abundance of damselfish species from north to south appear to be gradual, the determinants of the distributions of such species are likely to be related to latitude. Within the Red Sea the physical factors of surface temperature and salinity change gradually with latitude, salinity increasing from south to north and surface temperature decreasing from south to north (Morcos, 1970). The distributions of several species may be influenced by these changes. N. miryae, Po. trichourus and Pa. melas all become more common with increasing latitude. The within-reef distribution of Pa. melas is consistent with temperature being a controlling factor. In the central Red Sea it is restricted to the fore-reef and is commonest below 6m deep (Roberts and Ormond, in prep. a). In the Gulf of Aqaba, where surface temperatures are lower, its range extends into the shallows (< 2m deep) being common at the reef-edge and over the reef-flat. The surgeonfish Zebrasoma xanthurum and the butterflyfish Chaetodon paucifasciatus also have similar distribution patterns (Ormond et al., 1984). These observations were made during summer. In winter, surface water temperatures in the central Red Sea fall by some 5°C. If temperature is a controlling factor then these species may be able to occupy shallow regions of central Red Sea reefs during winter. However, during this survey no winter observations were made and this hypothesis remains untested.

In contrast to the above species, Po. leptus and N. cyanomos become increasingly common with decreasing latitude. Similarly, C. dimidiata and C. ternatensis are both much less common in the Gulf of Aqaba than throughout the rest of their geographical ranges. The distributions of these species also seem likely to be determined by latitude related factors.

Habitat The presence of an abrupt habitat discontinuity (Figure 1) where the continental shelf broadens makes it possible to identify at least some of those species within the Red Sea whose distributions are limited by the availability of particular habitats. Such species are characterised by large scale changes in abundance over a short distance to the north and south of this area in which deep, clearwater reefs give way to shallow, silty reefs. However, Carter and Prince (1981) have shown for plants that gradual change in continuous environmental variables, such as temperature, may produce abrupt limits to species' distributions by slight reductions in the viability of propagules. Given that fourteen (and possibly sixteen if uncommon species are included) out of 34 species show marked changes in abundance between north and south of the habitat discontinuity, and these changes occur in both directions, it is more likely that

reductions in propagule viability result from the abrupt change in habitat rather than, for example, gradual changes in salinity or temperature. The mechanism proposed by Carter and Prince (1981) may operate in the cases of C. dimidiata and C. ternatensis from the northern Red Sea into the Gulf of Aqaba, and for N. cyanomos in the southern Red Sea. Relatively abrupt changes in the abundance of these species were evident over regions in which there was no apparent habitat change.

Fringing reefs in the southern Red Sea differ markedly from those in the central & northern Red Sea (Figures 4 and 5)(Sheppard 1985). Water turbidity is much higher on southern reefs and they lack the lagoonal and fore-reef slope zones found on reefs to the north. The absence (or rarity) from southern reefs of eight species which are found on reefs in the north may be attributable directly to the absence of these zones. Chromis weberi, C. trialpha, C. pembrae, D. trimaculatus and Pl. lacrymatus are all most common on the fore-reef slope, whereas Chrysiptera annulata and A. sordidus were only observed in the lagoon zone, and S. nigricans usually observed in this zone, of reefs in the central & northern Red Sea (Roberts and Ormond, in prep. a).

Habitat effects also appear to control the distribution of Pristotis cyanostigma. This species is common on reefs in the southern Red Sea but was only observed at one site in the north, a turbid reef at the head of a large, shallow bay, suggesting that it is restricted to turbid habitats. Such habitats are uncommon in the central & northern Red Sea.

Simple presence or absence of particular habitats cannot explain the distributions of other species. Their distributions are explained best by a shifting of competitive dominance with changing habitat. Such shifts are suggested by reciprocal changes in the abundance of species with similar habitat or trophic requirements. For example, the planktivore Chromis dimidiata is the most abundant and ubiquitous damselfish species in the central & northern Red Sea, occurring in all zones of the fore-reef (Roberts and Ormond, in prep. a). However, it is absent from southern fringing reefs. N. xanthurus is the dominant planktivore on southern reefs but is present in only low numbers on clearwater reefs in the north. However, at one turbid water site in the northern Red Sea it was also abundant and C. dimidiata absent. Similarly, Amblyglyphidodon leucogaster is numerically dominant to A. flavilatus (both planktivores) in the central & northern Red Sea but is absent from the southern Red Sea, whilst A. flavilatus is abundant in the south (and at the turbid water northern site mentioned above). The territorial herbivore Pomacentrus trilineatus is uncommon and restricted to the lagoon zone of reefs in the central & northern Red Sea but is abundant on the shallow, fore-reef zone of reefs in the south. In contrast, Plectroglyphidodon leucozonus is abundant in the shallow fore-reef (1m terrace) zone of central & northern reefs but is

completely absent from southern fringing reefs despite the similarity of the shallow fore-reef in the south to the 1m terrace zone in the north. Chrysiptera unimaculata, another territorial herbivore, is probably also affected in this way. In the central & northern Red Sea it is abundant in lagoonal and 1m terrace habitats. With the absence of lagoonal habitats from the south it must occupy the fore-reef but is restricted to a very narrow band immediately seaward of the Sargassum zone, probably through competition with the larger Po. trilineatus and Po. aquilus.

One final species pair in which habitat changes may have altered competitive abilities is Dascyllus aruanus and D. marginatus. These omnivorous species inhabit colonies of branching corals but only rarely co-occur in the same colony. In central & northern regions D. aruanus is numerically dominant both in the lagoon and on patch reefs in shallow, sandy fore-reef zones. In the southern Red Sea the latter habitat is common but D. marginatus dominates, D. aruanus being rare.

Dispersal Barriers of unfavourable habitat may limit the dispersal of several species both within the Red Sea and from the Red Sea. For example, Po. aquilus is divided into two populations, one in the north and one in the south, separated by over 1000km. Brothers et al. (1983) calculated that the mean age at settlement of fourteen species of damselfish ranged between 21 and 24 days. Given that coastal currents within the Red Sea are typically less than 0.5 knots (Morley, 1975), it would take approximately 50 days for larvae from one population to reach the other (with unidirectional current flow) if Po. aquilus have a planktonic phase of similar duration. It seems likely therefore, that these populations are reproductively isolated. The presence of Po. aquilus on deep, clear reefs in the Gulf of Aqaba but not throughout the rest of the central & northern Red Sea seems puzzling. However, populations on these reefs need not be self-maintaining but may persist through a continued supply of recruits from habitats where Po. aquilus thrives (Dale, 1978). The shallow, turbid reefs of the Gulf of Suez are similar to reefs in the southern Red Sea on which Po. aquilus is abundant, and may provide such a source habitat.

Barriers of unfavourable habitat have probably also prevented the penetration of two endemic species, Chromis trialpha and Neopomacentrus miryae, from the Red Sea into the Gulf of Aden. These are both confined to the central & northern Red Sea. In the far southern Red Sea the water becomes very shallow towards the sill at the Straits of Bab el Mandab, reaching as little as 100m deep offshore (Morcos, 1970). Reefs in the region bordering the coast of North Yemen and the most southerly part of Saudi Arabia are sparse and poorly developed, this region being dominated by soft bottom habitats (A.R. Dawson Shepherd, pers. comm.). Therefore there are very few areas of suitable habitat available to species as 'stepping stones' to dispersal from the Red Sea, particularly species whose primary habitat

consists of well-developed, clearwater reef. The six endemic species whose ranges do extend into the Gulf of Aden or beyond (Table 1) are all common on turbid reefs of the southern Red Sea. Po. albicaudatus is an exception in that it is common on turbid reefs in the south but has not yet been recorded outside the Red Sea (Allen and Randall, 1980).

Community composition Cluster analyses of both species presence/absence data and quantitative transect data show a large dissimilarity between damselfish communities inhabiting the central & northern and southern regions of the Red Sea. Comparison of the analysis based on species presence/absence with that based on gross reef morphology indicates that some of this difference may be related to structural habitat features. Coral reef fishes are dependent on the substratum for shelter (protection from predators), food, and in some cases reproduction. Several studies have shown relationships between aspects of reef structure, such as structural complexity or composition of the substratum, and the resident fish community (Risk, 1972; Luckhurst and Luckhurst, 1978; Carpenter et al., 1981; Roberts and Ormond, in prep. b). Coral reef structure is almost certainly dependent more directly on environmental conditions such as wave action, water temperature, tidal range, bottom topography and turbidity, than is fish community structure (Bradbury and Young, 1981; Dollar, 1982; Done, 1982; Sheppard, 1982; Mergner, 1984). Within the Red Sea the latter factors of bottom topography and turbidity are probably most important (Sheppard, 1985; Sheppard and Sheppard, 1985), the shallow inshore waters of the south contrasting with the deep inshore waters of central & northern regions. These shallow conditions have led to high levels of water turbidity and this has a major influence on the composition of the coral community (Basson et al., 1977; Sheppard, 1985; Sheppard and Sheppard, 1985). These changes in coral community structure and reef structure probably have a strong influence on damselfish community structure. The clustering of the only two turbid reefs sampled in the northern Red Sea with the turbid reefs of the southern Red Sea (Figure 6) on the basis of species presence/absence, underlines the importance of turbidity in structuring coral, and hence fish, communities.

The Red Sea is effectively a peninsula of the Indian Ocean and hence might be expected to conform to the 'peninsula effect' of decreasing species richness approaching its extremities (south to north)(MacArthur and Wilson, 1967). Coupled with this there is a latitudinal gradient of 13° from south to north along the Saudi Arabian coast and this might also be expected to add to a decline in species richness from south to north (Pianka, 1966). However, dividing the Saudi Arabian coast into three regions of approximately equal size, north, central and south, there were respectively 27, 26 and 24 species observed in each region. Habitat factors thus appear to

override the effects of decreasing latitude and increasing isolation from the species source (Indian Ocean) in Red Sea damselfish communities. The lower areal coverage of inshore reefs in the south, and the relative structural simplicity of these reefs compared with those in central and northern regions are almost certainly the most important of these habitat factors. However, the islands and reefs of the Farasan Archipelago and Farasan Bank lie 50 to 130km offshore from the southern coast of Saudi Arabia, and it will be necessary to thoroughly survey these before final conclusions can be drawn about patterns of species distribution and richness in the eastern Red Sea.

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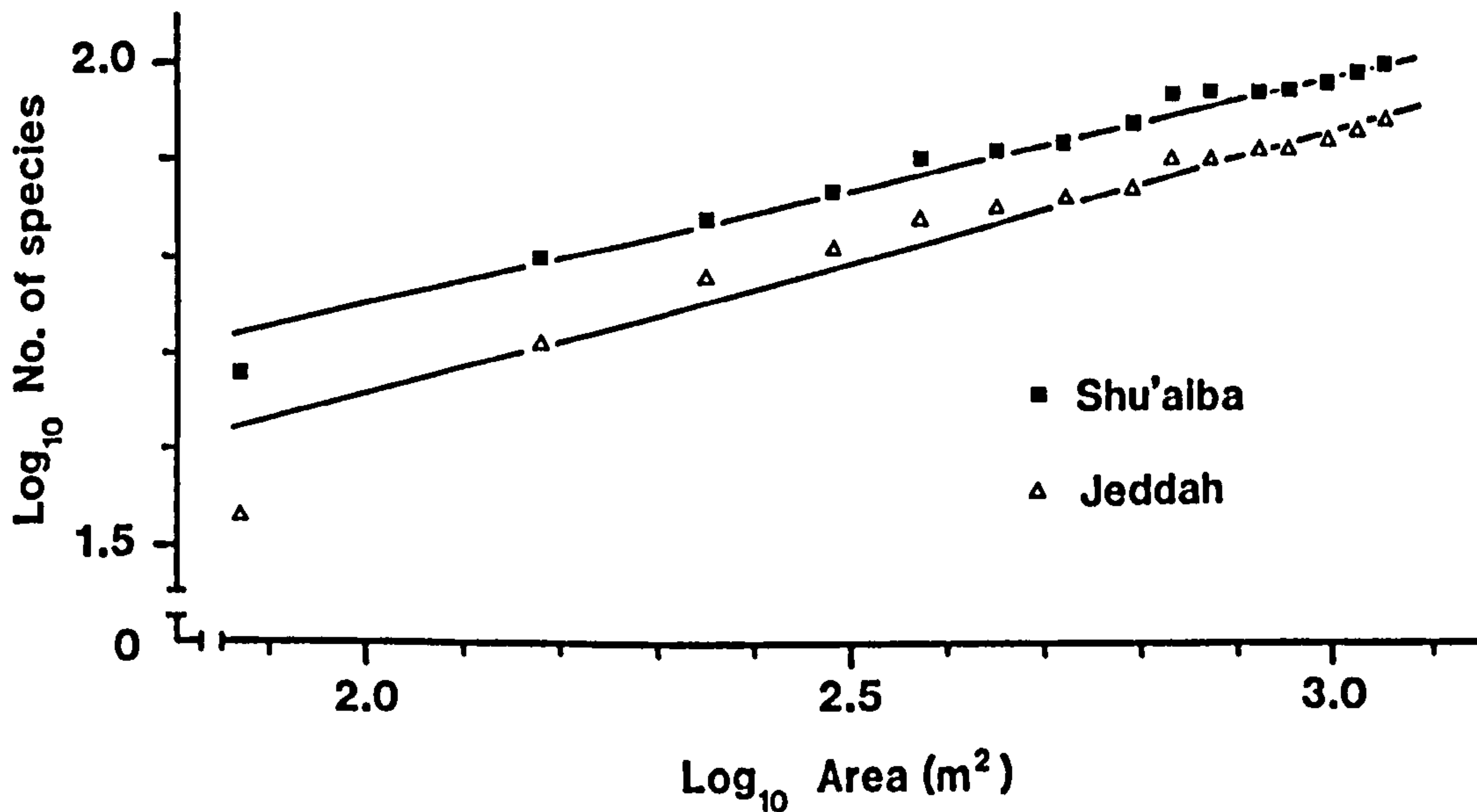
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ADDITIONAL NOTE: In addition to damselfish, species from other families of fish were counted in the study of species-area relationships at Jeddah and Shu'aiba described in the preceding chapter. These were Labridae, Chaetodontidae, Pomacanthidae, Tetraodontidae, Balistidae, Acanthuridae, Scaridae, Siganidae, Lethrinidae, Lutjanidae, Serranidae, Cirrhitidae, Holocentridae, Scorpaenidae, Cueslonidae, Ostraciidae and Diodontidae. The full species-area relationship is shown above. The fitted regression lines have slopes corresponding to a 17% increase in the number of species with each doubling in area at Shu'aiba and 20% at Jeddah. Hence, minimum sampling area (area sampled after which doubling the sampling area does not increase the number of species by more than 10%) cannot be determined from this plot.

Chapter 2

**Biogeography of Red Sea surgeonfish (Acanthuridae)
and parrotfish (Scaridae) on the Saudi Arabian coast.**

ABSTRACT

This paper describes large-scale variation in the structure of communities of herbivorous fishes on the Red Sea coast of Saudi Arabia. Species of surgeonfish (Acanthuridae) and parrotfish (Scaridae) were recorded at 48 and 46 sites respectively, covering around 1800km of coastline. Previous work has suggested that the abundance and species richness of herbivorous fishes on coral reefs is broadly correlated with the productivity of turf algae. Evidence from a number of sources suggest that productivity of coastal waters is considerably higher in the southern Red Sea than in central & northern regions. To test this, the numbers of surgeonfish and parrotfish were counted along a 100 x 5m transect laid at 1.5m deep along the reef-edge at some 75% of the sites censused. Community composition data were analysed using numerical classification. Habitat differences between southern and central & northern regions of the Saudi Arabian coast, primarily differences in reef structure and water quality, had a major influence on community composition of both surgeonfish and parrotfish. Whilst numbers of parrotfish per site did not differ significantly between central & northern and southern regions, surgeonfish were significantly less numerous in the south. In both families, the number of species observed per site was greater in central & northern regions than in the south. These data do not support the view that herbivore abundance or species richness are correlated with the productivity of turf algae (although direct measurements of productivity were not made in this study). Rather, the influence of habitat differences between regions of the Saudi Arabian coast appears to have a greater effect on communities of these fishes.

INTRODUCTION

This study was conducted as part of a survey of coral reef fish communities on the reefs of the Red Sea coastline of Saudi Arabia. In a companion study, Roberts and Ormond (in prep.) have documented distribution patterns of damselfish (Pomacentridae) species over this region. They found that communities inhabiting reefs in the southern Red Sea were very different from those inhabiting reefs in central & northern regions. This change is attributable primarily to differences in habitat between these regions, the central & northern Red Sea being characterised by deep, clearwater reefs and the southern Red Sea by shallow, turbid reefs (Sheppard, 1985; Sheppard and Sheppard, 1985). Changes in water temperature and salinity from south to north may also be involved.

Productivity in the southern Red Sea appears to be considerably greater than in the oligotrophic waters of the central & northern Red Sea and this is mainly due to inflow from the south of relatively nutrient rich water from the Gulf of Aden (Morley, 1975; Morcos, 1970; Weikert, 1980). This increase in productivity is reflected by an increase in the standing crop of macro-algae and turf algae from north to south (Sheppard, 1985; CR, personal observations). Russ (1984a;b;c) has documented patterns in the distribution of herbivorous fishes across the central region of the Great Barrier Reef and concluded that there was a broad correlation between the availability of turf algae and the abundance of such fishes. The present study investigates the composition of communities of parrotfish (Scaridae) and surgeonfish (Acanthuridae) on reefs from north to south along the Saudi Arabian coast with the aims of (1) describing patterns of community change throughout the region and comparing these with those found in damselfish communities (Roberts and Ormond, in prep.), and (2) relating changes in community structure to the influences of habitat, primary productivity and other biogeographical influences on species distribution.

METHODS AND STUDY AREA

The study area

The Red Sea is a long, narrow, deep basin which runs in a NNW to SSE direction between Africa and the Arabian peninsula. Because of its location between two large areas of desert, it is characterised by high rates of evaporative water loss. There are no permanent rivers flowing into the Red Sea and little direct precipitation, and so this loss is not balanced by freshwater input. Consequently, salinities are much higher than in the adjacent Indian Ocean. This evaporative water loss leads to a net inflow of water from the Gulf of Aden through the Straits of Bab el Mandab, sea level being around 35cm higher in the south than in the north, creating a north to south salinity gradient (37 p.p.t. in the south to 41 p.p.t. in the north; Morcos, 1970).

Surface currents are primarily wind-driven with a seasonal reversal in direction of flow (Patzert, 1974; Morley, 1975; Mustafa *et al.*, 1980). For seven months of the year (October to April) currents flow NNW under the influence of the winter monsoon. From May to September the prevailing current flow is in a SSE direction.

As the Red Sea covers some 18° of latitude, there is a north to south gradient in surface water temperature. During July, average surface water temperature is around 25°C in the Gulf of Aqaba compared with 31°C in the southern Red Sea, whilst in January average temperatures range between 18°C in the north and 26°C in the south (Morcos, 1970).

More detail on the complex oceanographic conditions and geological history of the Red Sea are given elsewhere (Morcos, 1970; Girdler, 1984; Johnson and Feltes, 1984; Winterbottom, 1985; Edwards, in press).

Methods

The surgeonfish species present were recorded at 48 sites and parrotfish species at 46 sites along the Saudi Arabian coast (Figure 1). At each site a 30 minute swim was made whilst snorkelling and a 20 minute swim using SCUBA, covering all reef zones, and species of surgeonfish and parrotfish observed recorded. In addition, at 37 sites for parrotfish and 36 sites for surgeonfish, quantitative data were collected by counting fish along a 100 x 5m transect laid at a depth of approximately 1.5m on the fore-reef (corresponding to the reef-edge). This transect was marked with a 100m leaded rope and the width was visually estimated as 2.5m either side of the line. Parrotfish and surgeonfish were counted on separate swims along the transect. This technique was the same as that used by Roberts and Ormond (in prep.) to census damselfish communities in the same region allowing direct comparability of results. However, in contrast to damselfish, it was

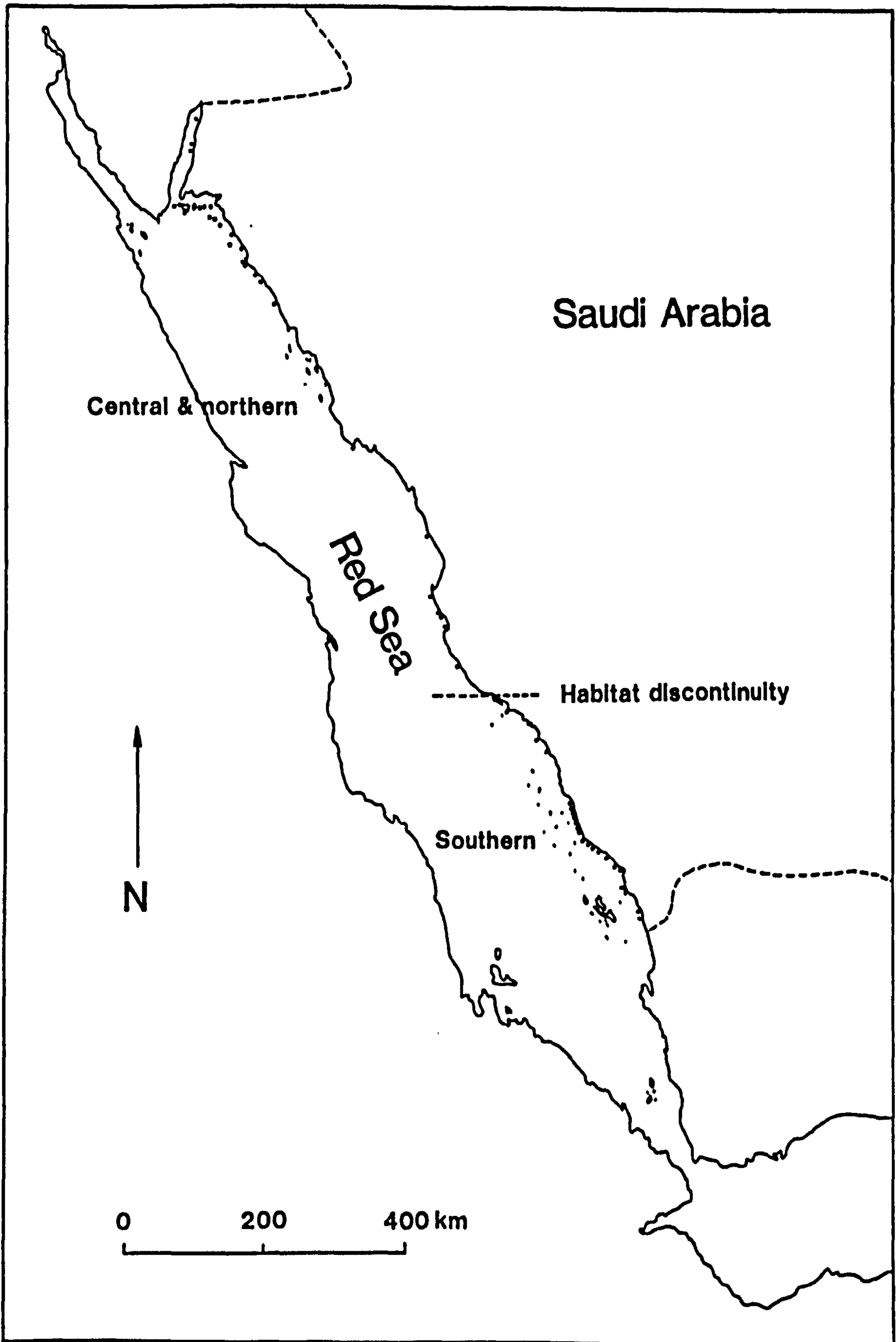


Figure 1: Map of the Saudi Arabian Red Sea coast showing the locations of the study sites. The division into central & northern and southern regions used in this study is based on the location of the habitat discontinuity which marks a changeover between deep, clearwater reefs in the north and shallow, turbid reefs in the south.

<u>SPECIES</u>	<u>DISTRIBUTION*</u>	<u>FOOD HABITS**</u>	<u>REFERENCES</u>
Surgeonfish			
<u>Acanthurus nigricans</u>	Red Sea + G of A	SS/SC	Pers. obs.
<u>A. nigrofuscus</u>	Indo-Pacific	SC	1,2
<u>A. sohal</u>	Red Sea to A.G.	SC	4,9
<u>Ctenochaetus striatus</u>	Indo-Pacific	SFS	1,2,3,5
<u>Naso brevirostris</u>	Indo-Pacific	LC/P	1,2,3
<u>N. hexacanthus</u>	Indo-Pacific	P	1,2,6
<u>N. lituratus</u>	Indo-Pacific	LC	2,3,5
<u>N. unicornis</u>	Indo-Pacific	LC	1,2,5
<u>Z. veliferum</u>	Indo-Pacific	LC/SC	1,2,5
<u>Z. xanthurum</u>	Red Sea to A.G.	SC	Pers. obs.
Parrotfish			
<u>Bolbometopon muricatum</u>	Indo-Pacific	C	2,3,7
<u>Calotomus viridescens</u>	Red Sea	LC(seagrass)	Pers. obs.
<u>Cetoscarus bicolor</u>	Indo-Pacific	S	2,5
<u>Hipposcarus harid</u>	Indian Ocean	S	Pers. obs.
<u>Scarus ferrugineus</u>	Red Sea + G of A	S/C	8
<u>S. frenatus</u>	Indo-Pacific	S	2
<u>S. fuscopurpureus</u>	Red Sea	S	Pers. obs.
<u>S. ghobban</u>	Indo-Pacific	S	2
<u>S. gibbus</u>	Indo-Pacific	S	2
<u>S. niger</u>	Indo-Pacific	S	2
<u>S. psittacus</u>	Indo-Pacific	S	2,8
<u>S. sordidus</u>	Indo-Pacific	S	2,5,6

Table 1: Surgeonfish and parrotfish observed during this study. *Distributional ranges are those given in Randall (1983). **Feeding categories are as defined by Russ (1984b); SS = sand sucker, SC = small cropper, LC = large cropper, SFS = sucker of fine sediments, S = scraper, P = planktivore, and C = corallivore. References are: (1) Jones (1968), (2) Russ (1984b), (3) Randall (1983), (4) Vine (1974), (5) Hiatt and Strasburg (1960), (6) Hobson (1974), (7) Smith (1959), (8) Randall and Ormond (1978), and (9) Roberts (1985).

found to be unsatisfactory in assessing relative abundances of parrotfish and surgeonfish species due to high between-count variability (Roberts, unpublished data). This is because these species are much more vagile than damselfish species, moving over relatively large areas of reef. This has the effect of increasing sampling variance because the home-ranges of most individuals lie only partially within the transect, whereas, except for those at the edges, the small home-ranges of damselfish are mostly contained within the transect. Hence, counts for each species observed on the transect were summed to give an approximate measure of overall abundance for each family.

The extensive tract of reefs and islands in the southern Red Sea, the Farasan Bank and Archipelago, were not visited during this survey. However, a large number of underwater photographs were taken in this region during a previous survey (Ormond et al., 1986). These were analysed for the presence of surgeonfish and parrotfish species in order to give some coverage of this area.

Cluster analyses were run on species presence/absence data using Ward's error sum of squares method with Euclidean distance as a similarity measure (Wishart, 1978).

RESULTS

Algal standing crop

Saudi Arabian Red Sea fringing reefs are often characterised by the presence of a band of macro-algae along the reef crest (Roberts and Ormond, in prep.; Sheppard, 1985). This consists predominantly of Sargassum but can include varying amounts of Turbinaria. Within this zone the density of plants appears relatively homogeneous with all available space filled. The width of this zone is thus used here as an estimate of macro-algal standing crop and is shown in Figure 2 for all the sites visited. There is a marked increase in macro-algal standing crop with decreasing latitude. Reefs in the northern Red Sea totally lack a Sargassum zone whilst those in the south typically have a broad and well-developed zone. This increase in the width of the Sargassum zone is matched by an increase in the heights of individual plants. Qualitative observations indicate that plants in the central Red Sea are typically 0.3-0.6m long whilst those in the southern Red Sea frequently reach 1.5-2m long. This may be partially a result of increasing tidal amplitude from the central to the southern Red Sea (Morcos 1970). However, tidal range also increases from central to northern regions and so the absence of the Sargassum zone from northern reefs cannot be attributed to tidal patterns.

The standing crop of turf algae was also higher on southern reefs than on reefs in the central & northern Red Sea. Samples were taken of the algae within the territories of the surgeonfish Acanthurus sohal from one site in the central Red Sea and one site in the south. These sites appeared typical of others throughout each region. Mean standing crop at the central Red Sea site was $14.9 \pm 11.0 \text{ g/m}^2$ (ash-free dry weight)(n = 14) compared with $110.6 \pm 14.4 \text{ g/m}^2$ (n = 5) at the southern site. The composition of the turf algae also differs. It is composed mainly of filamentous green species in central & northern regions whilst in the south it contains a large proportion of red and fleshy algae.

Parrotfish and surgeonfish communities

Abundance Figures 3 and 4 show the total numbers of surgeonfish and parrotfish counted on a 100 x 5m transect at each site. There is considerable between-site variability in the abundance of fishes from both families. However, dividing the Red Sea into two regions, central & northern and southern, at a point corresponding to the habitat discontinuity previously identified (Roberts and Ormond, in prep.), there are significantly fewer surgeonfish per site in the south than in central & northern regions ($78.7 \pm 12.7 \text{ S.E.}$ vs $36.9 \pm 7.0 \text{ S.E.}$, t-test, $P < 0.05$; n = 36). In contrast, similar numbers of parrotfish were observed at sites in both regions ($25.0 \pm 3.2 \text{ S.E.}$ vs 29.5 ± 5.3

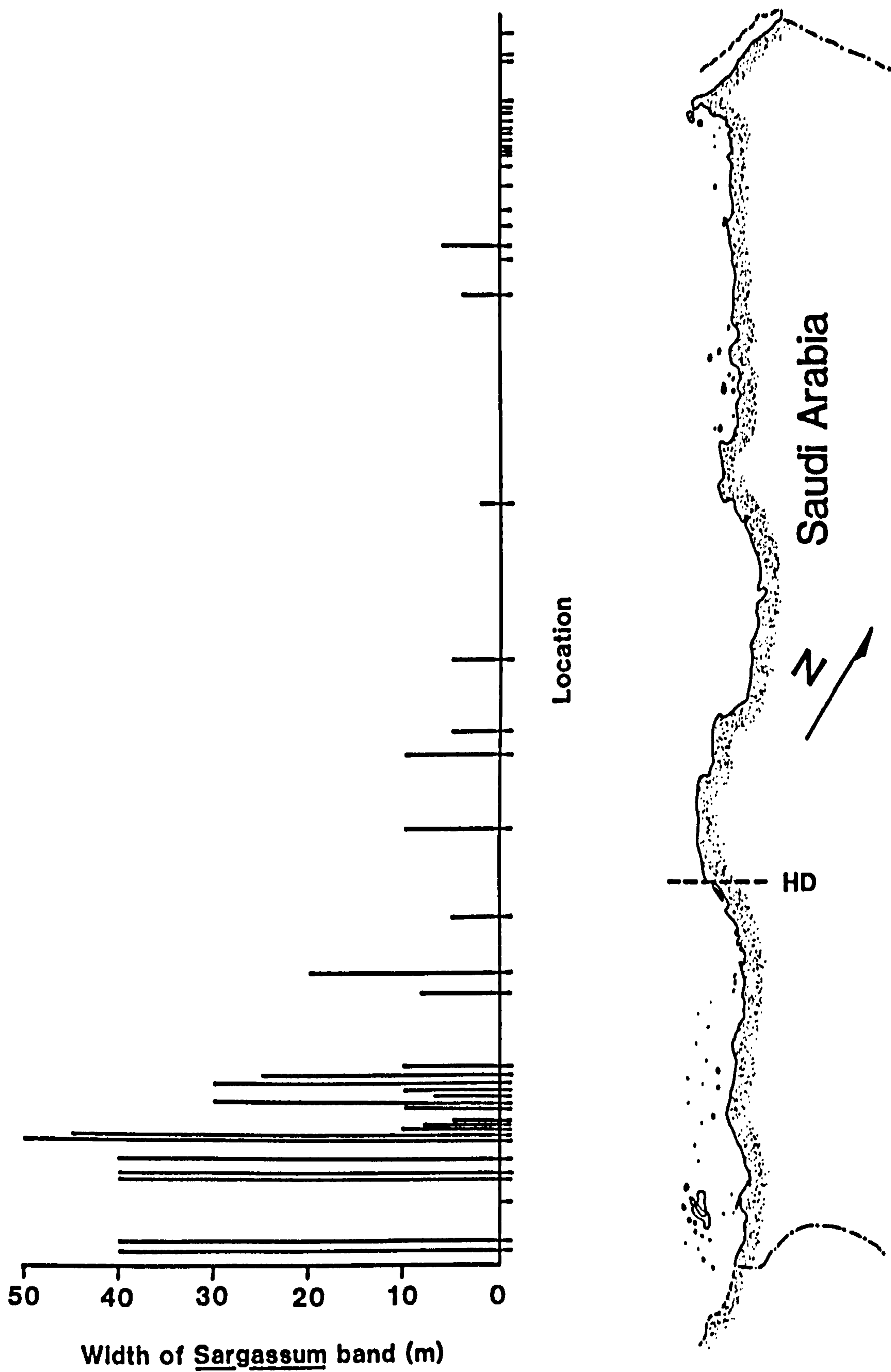


Figure 2: Width of the band of Sargassum algae over the reef crest at sites along the Saudi Arabian Red Sea coast. 'HD' shows the location of the habitat discontinuity.

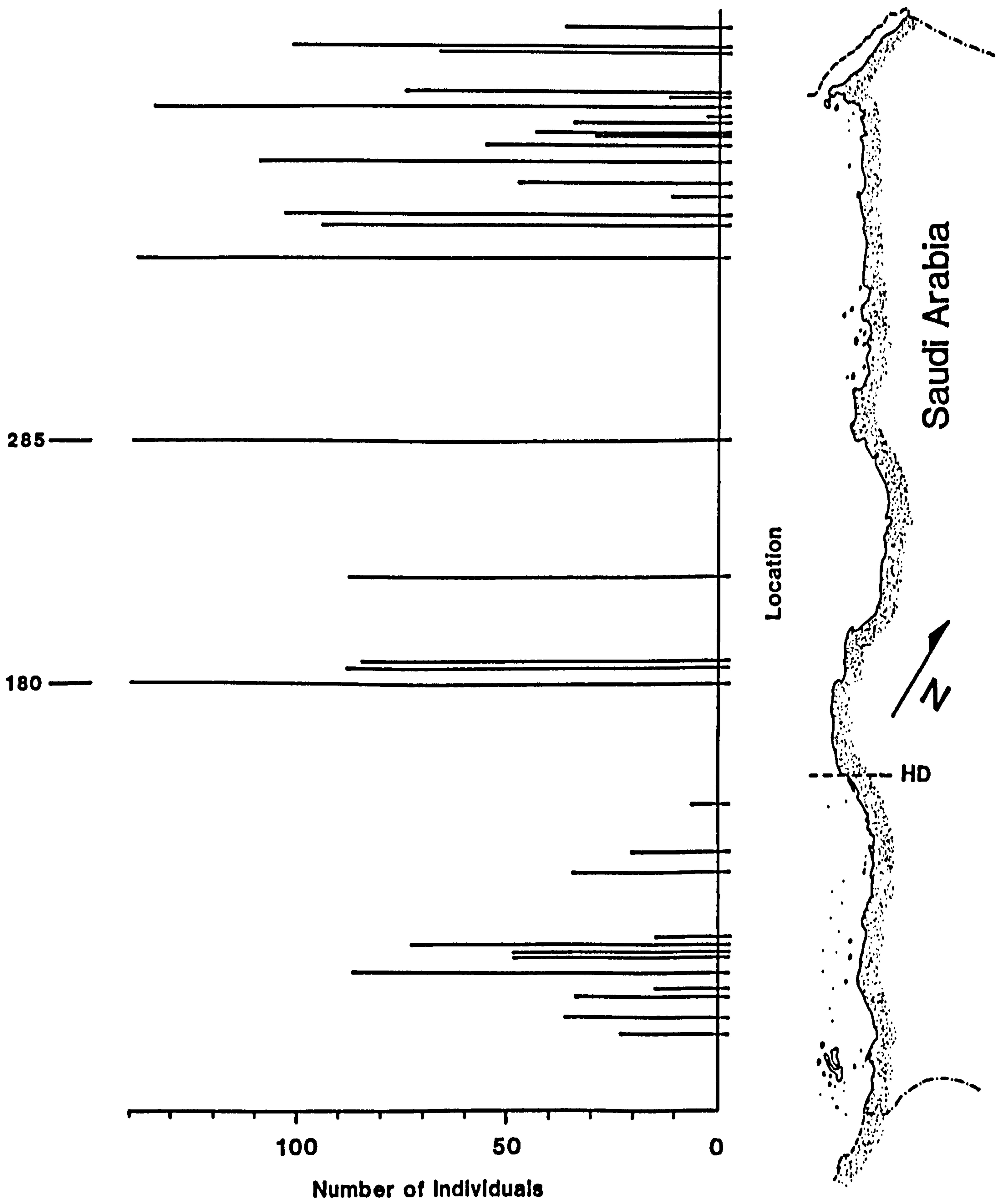


Figure 3: Total surgeonfish abundance on 100 x 5m transects. 'HD' shows the location of the habitat discontinuity.

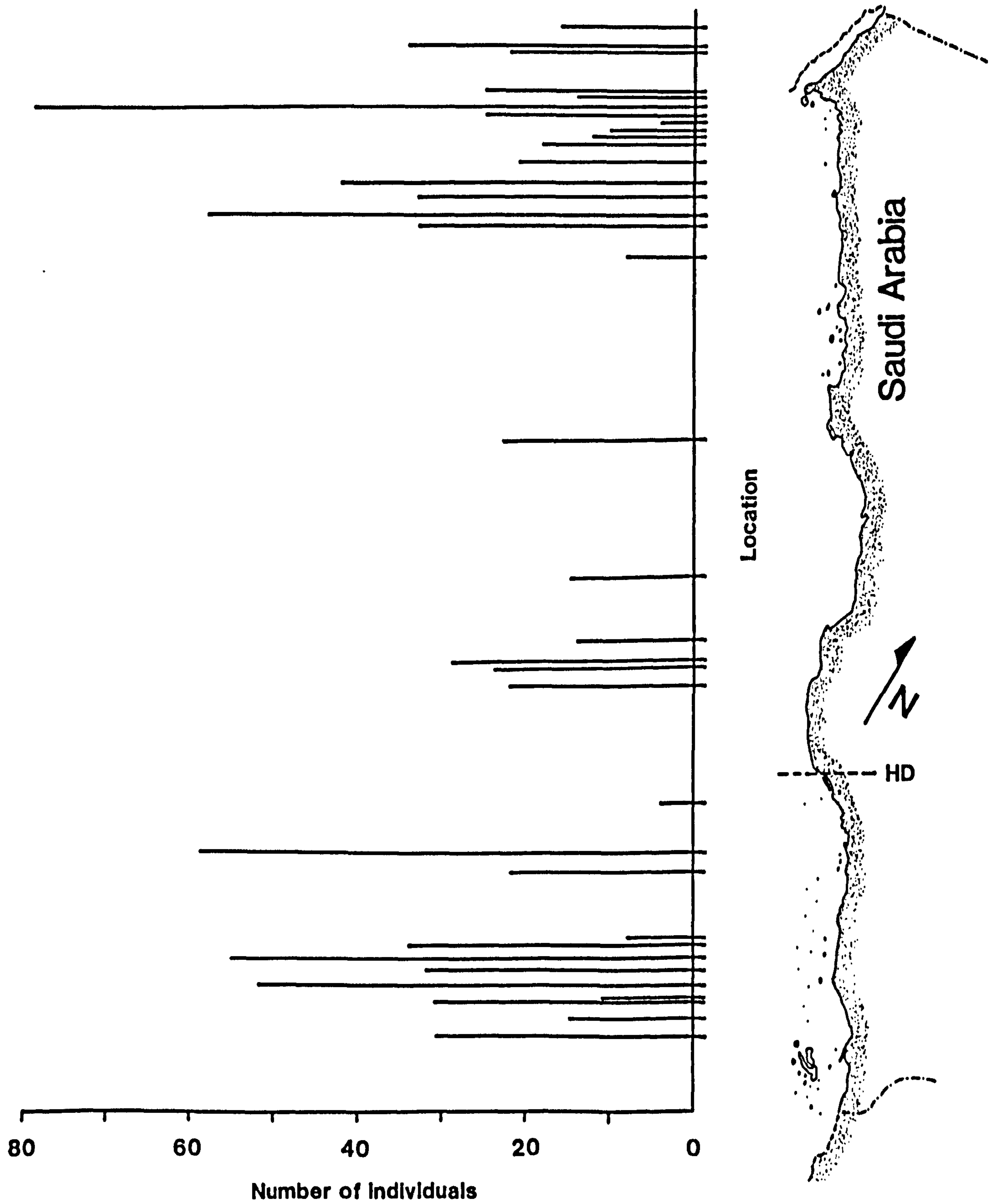


Figure 4: Total parrotfish abundance on 100 x 5m transects. 'HD' shows the location of the habitat discontinuity.

S.E., t-test, $P > 0.10$; $n = 37$).

Species richness Figures 5 and 6 show the numbers of species of surgeonfish and parrotfish observed at each site. In both families there were significantly more species observed per site in the central & northern Red Sea than in the southern Red Sea. On average there were 7.5 ± 0.5 S.E. parrotfish per site in central & northern regions versus 4.4 ± 0.5 S.E. per site in southern regions (t-test, $P < 0.001$; $n = 37$). Similarly there were on average 5.3 ± 0.4 S.E. surgeonfish per site in central & northern regions versus 3.0 ± 0.3 S.E. in southern regions (t-test, $P < 0.001$; $n = 36$).

Species distributions

Surgeonfish Figure 7 shows the distributions of surgeonfish species along the Red Sea coast of Saudi Arabia. Three of the ten surgeonfish species recorded during this survey were common on reefs throughout the whole of this region. They were Acanthurus sohal, Ctenochaetus striatus and Zebrasoma veliferum, although A. sohal is scarce in the Gulf of Aqaba.

Four species which are common in the central & northern Red Sea were absent or very rare on inshore reefs in the south. They were Naso lituratus, N. unicornis, Acanthurus nigrofuscus and Zebrasoma xanthurum. The former three species occur in similar densities throughout their ranges whereas Z. xanthurum is considerably more common in the Gulf of Aqaba than elsewhere in the central & northern Red Sea (unpublished data). Two other species of the genus Naso, N. brevirostris and N. hexacanthus were uncommon, being recorded at only three and five sites respectively. However, where present, N. hexacanthus was observed in relatively large schools. All of the records for both of these species were from sites in the central & northern Red Sea (although there are photographic records from offshore reefs further south, Figure 7).

Only one species, Acanthurus nigricans, was more common in the southern Red Sea than in central & northern regions. This difference was very pronounced, A. nigricans being observed at only four of 27 sites in the central & northern Red Sea but at all of the 21 sites visited in the southern Red Sea. It appears to thrive in the turbid conditions prevailing in the latter region.

Parrotfish Six of the twelve parrotfish species observed during this survey were found on reefs throughout the entire Saudi Arabian coast (Figure 7). They were Scarus ferrugineus, S. ghobban, S. niger, S. psittacus, S. sordidus and Hipposcarus harid. Of these, S. niger and S. sordidus were not observed at the most turbid water sites whilst, in contrast, S. ghobban was more often observed at such sites than on less turbid reefs. This latter species is scarce in the Gulf

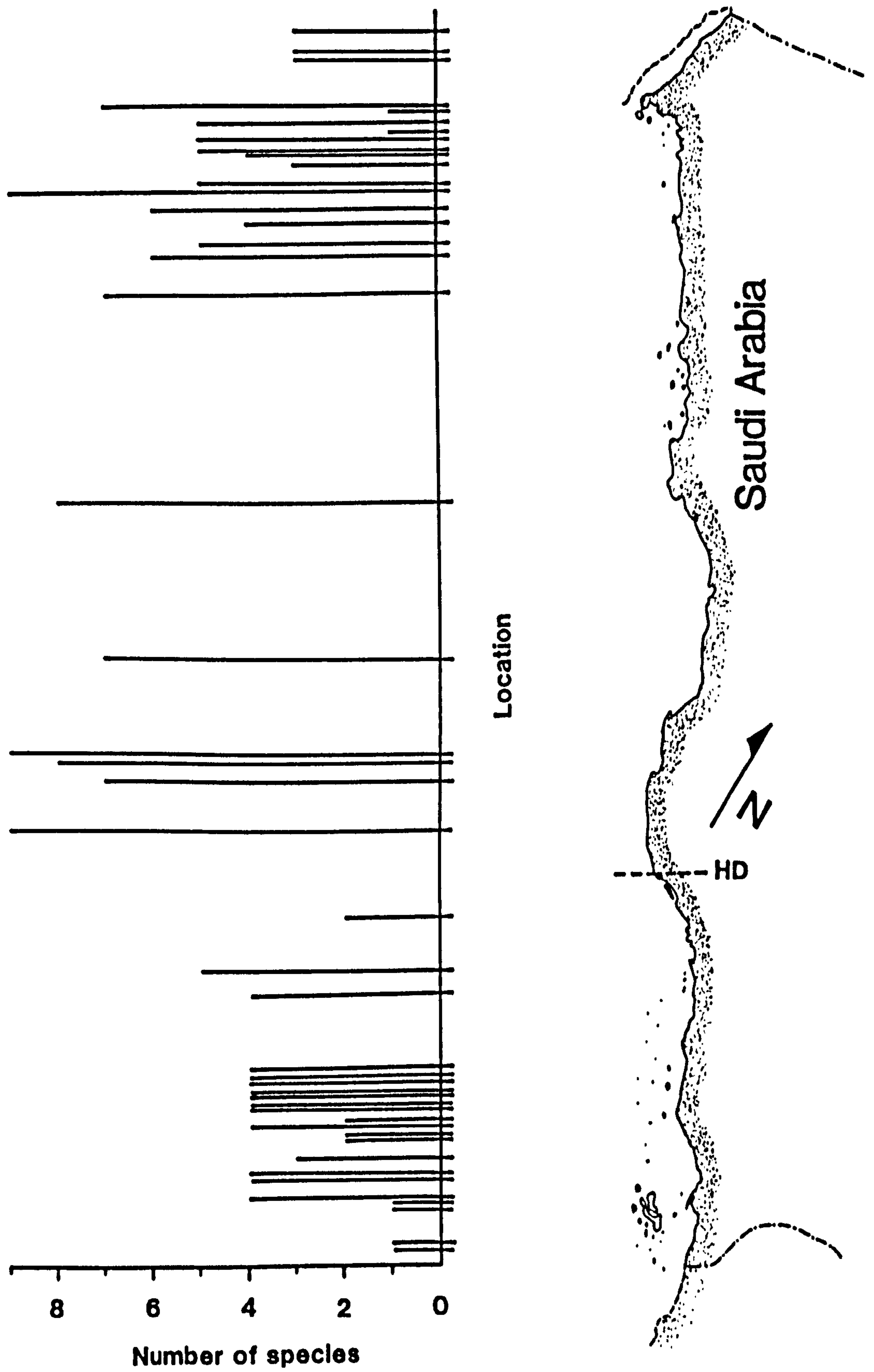
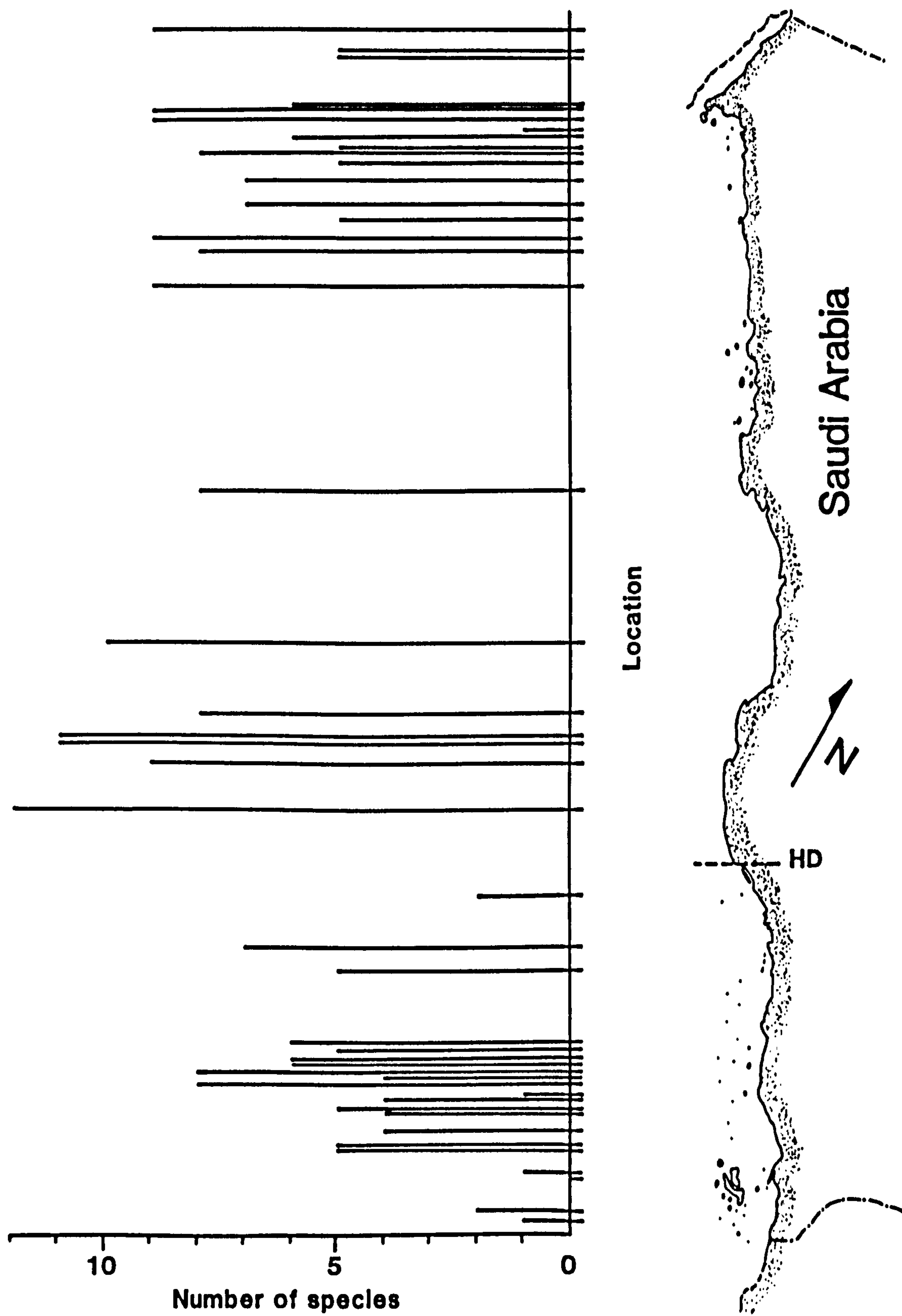


Figure 5: Species richness of surgeonfish at sites along the Saudi Arabian Red Sea coast. 'HD' marks the location of the habitat discontinuity.



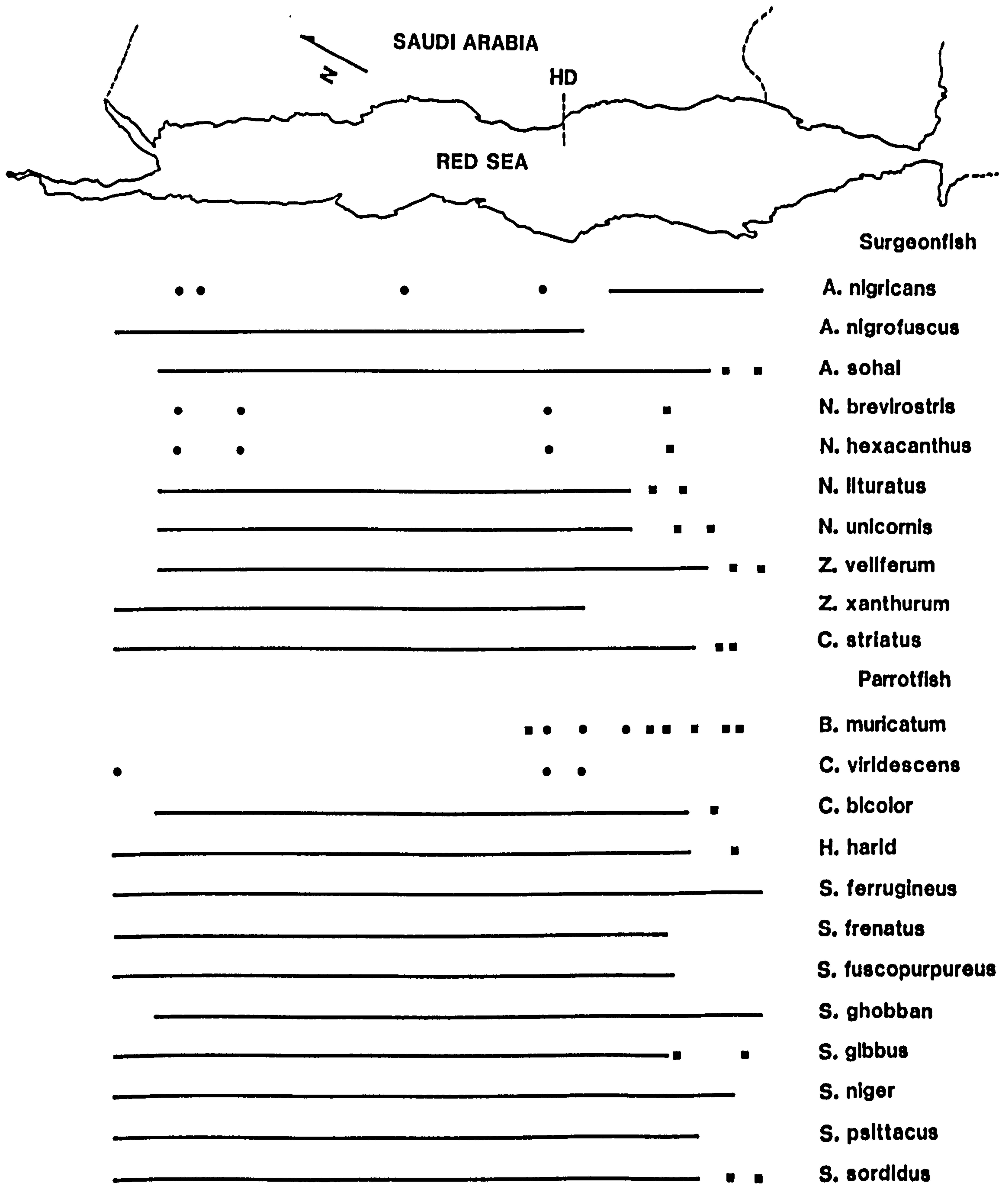


Figure 7: Distributions of surgeonfish and parrotfish species along the Saudi Arabian Red Sea coast. Circles show the sites at which species were observed for those species which were only observed at a small number of sites. Squares represent photographic records of species from offshore and island reefs in the southern Red Sea. 'HD' marks the location of the habitat discontinuity on the Saudi Arabian coast.

of Aqaba. S. ferrugineus was considerably more common and S. psittacus less common on southern reefs than on those in central & northern regions.

Four species were common in the central & northern Red Sea but were rare on inshore reefs of the south. They were Scarus frenatus, S. fuscopurpureus, S. gibbus and Cetoscarus bicolor. The latter species was scarce in the Gulf of Aqaba. Calotomus viridescens, a species endemic to the Red Sea, was only observed at three sites but was relatively common at two of these. All three sites were in the central & northern Red Sea.

As was the case for surgeonfish, only one species of parrotfish was more common on southern than on central & northern reefs. This was Bolbometopon muricatum, a large coral feeding species. However, during this survey it was only observed on fringing reefs at five sites, the most northerly record being from Jeddah. During a previous survey (Ormond et al., 1984) it was found to be common on offshore and island reefs in the southern Red Sea as far south as the Farasan Archipelago. In this previous survey it was observed as far north as Aiqa island, 70km north of Jeddah.

Community composition

Surgeonfish Cluster analysis of surgeonfish species presence/absence data reveals four clusters when split at a Euclidean distance of 2.00 (Figure 8). There is a major division between sites in the central & northern and the southern Red Sea. These two main clusters are each subdivided into two. They correspond to (1) northern Red Sea onshore and island reefs, (2) central & northern Red Sea species rich sites, (3) southern Red Sea turbid and algal reefs, and (4) southern Red Sea clearwater and 'classic' fringing reefs (see Sheppard, 1985 for descriptions of these reef types from the southern Red Sea).

One site from the northern Red Sea (Aynunah Bay) is classified with sites from the south (cluster 3, turbid and algal reefs) and this was a highly turbid reef at the head of a large, shallow bay.

Parrotfish Cluster analysis of parrotfish species presence/absence data again reveals four clusters, this time when split at a Euclidean distance of 1.00 (Figure 9). Cluster 1 corresponds to relatively species rich sites in the central & northern Red Sea (7-12 species per site), whilst cluster 2 corresponds to species poor sites from this region (5-6 species per site) and is more similar to sites in the southern Red Sea than to other sites in central & northern regions. Cluster 3 consists of a mix of turbid, clearwater and 'classic' fringing reefs from the southern Red Sea, and cluster 4 consists of turbid and algal reefs from the south but also includes the turbid Aynunah Bay site and one other site from the northern Red Sea.

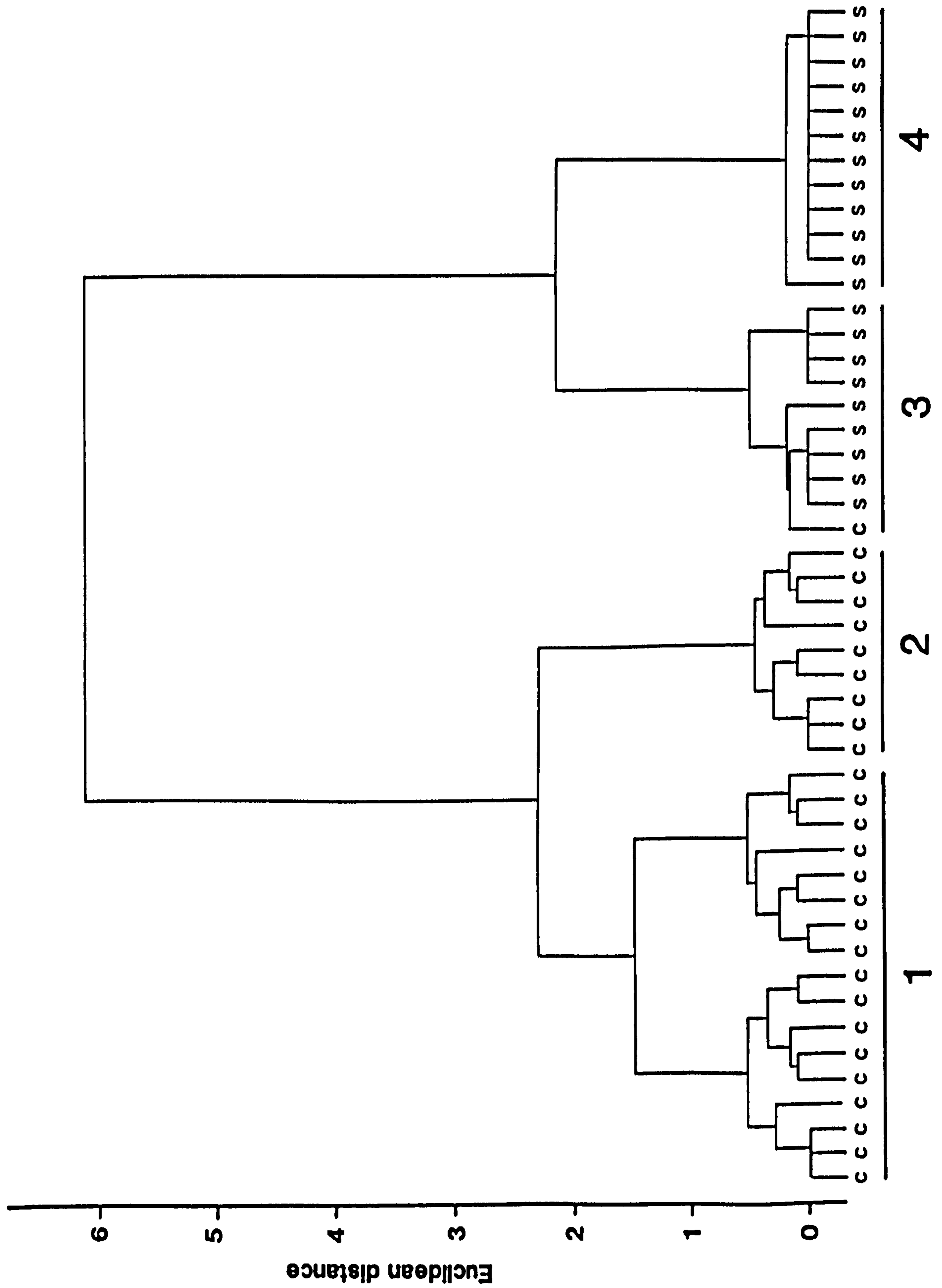


Figure 8: Classification of sites based on surgeonfish species presence/absence data, using Ward's error sum of squares method. Four clusters are defined at a Euclidean distance of 2.00. Sites marked 'C' are from the central & northern Red Sea and 'S' from the southern Red Sea.

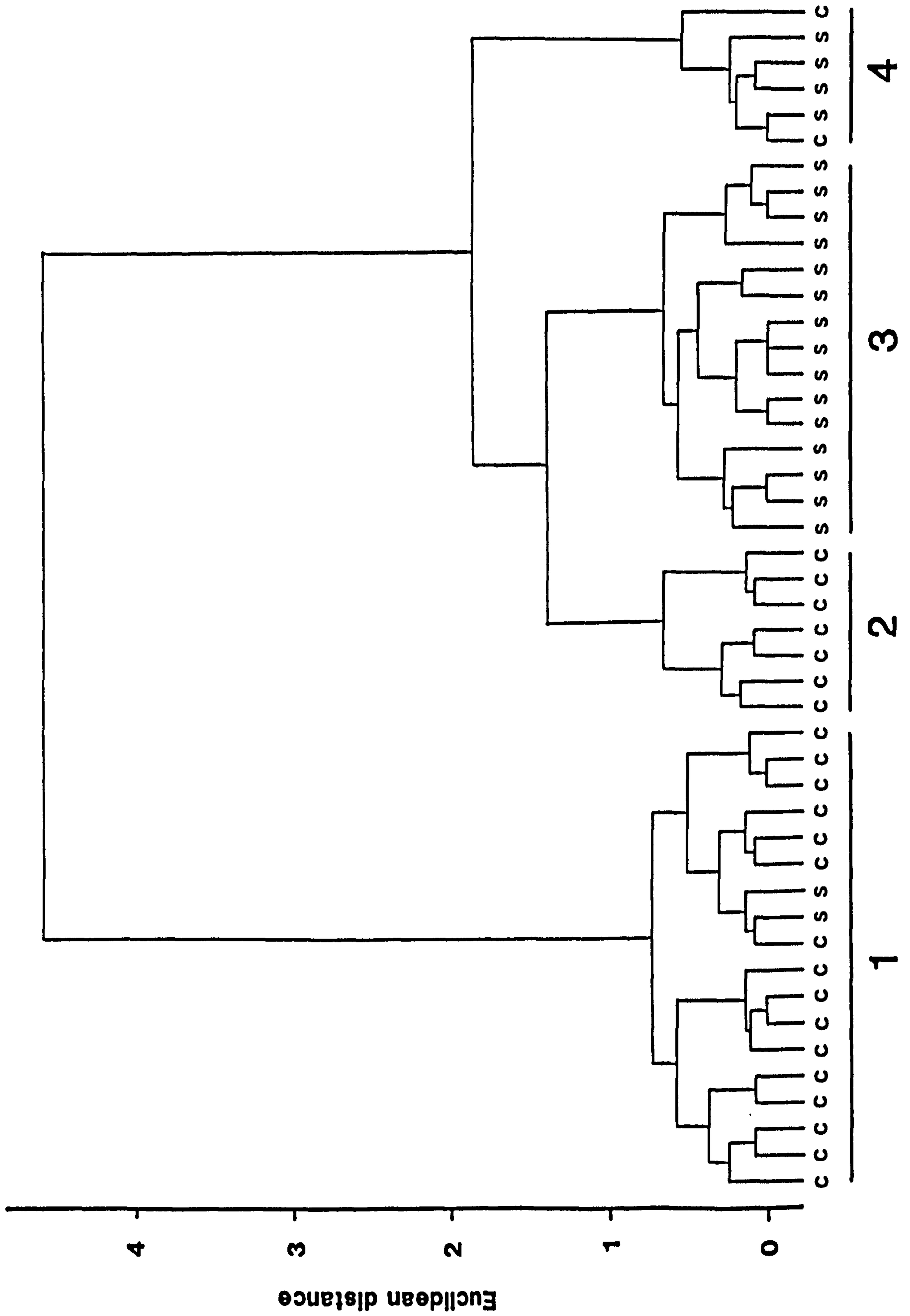


Figure 9: Classification of sites based on parrotfish species presence/absence data. Four clusters are defined at a Euclidean distance of 1.00. Sites marked 'C' are from the central & northern Red Sea and 'S' from the southern Red Sea.

DISCUSSION

Russ (1984a;b) in his studies of the distribution of herbivorous reef fishes in the central section of the Great Barrier Reef, concluded that surgeonfish and parrotfish species richness and abundance were significantly greater on mid- and outershelf reefs than on inshore reefs. This pattern correlated broadly with the productivity of turf algae, productivity being some 10-15 times greater on mid- and outershelf reefs than on inshore reefs. Several studies, relying mostly on indirect evidence have suggested that the open waters of the southern Red Sea are more productive than those of central & northern regions (Gordeyeva, 1970; Morley, 1975; Thiel, 1980; Weikert, 1980; Shimkus and Trimonis, 1983). This is thought to be primarily due to nutrient rich waters from the Gulf of Aden flowing in through the Straits of Bab el Mandab (Morley, 1975). For example, nitrate levels in the upper 50m of the water column are five times greater in the Gulf of Aden than in the central Red Sea. Evaporative water losses from the Red Sea and winds result in an inflowing surface current through the Straits of Bab el Mandab for around seven months of the year (Morcos, 1970; Patzert, 1974). There is very little nutrient input into the Red Sea through terrestrial run-off but southern Saudi Arabian coastal regions do receive more rainfall than those further north and this may partially contribute to higher nutrient levels in the south (Ormond et al., 1986)

Further evidence that productivity is higher in the south is provided by the much higher standing crop of macro-algae on reefs in this region than on reefs further north. Johannes et al. (1983) note that growth of macro-algae is favoured over corals by high nutrient concentrations. However, this evidence should be treated with caution since algal standing crop and productivity are only sometimes but not always correlated (Wanders, 1976a;b; Hatcher and Larkum, 1983; Russ, 1984a). Reefs in the south also have a higher standing crop of turf-algae.

If Russ's (1984a) findings hold true for the Red Sea then we would expect an increase in the abundance and species richness of herbivorous fishes from north to south following the (probable) gradient of increasing productivity. However, this is not the case. The average per-site species richness of both surgeonfish and parrotfish was significantly lower in the southern than in the central & northern Red Sea. Similarly, there were significantly fewer surgeonfish counted per transect at sites in the south than in central & northern regions, whilst the abundance of parrotfish per transect did not differ significantly between the two regions.

Fishes of the family Siganidae, of which there are four species in the Red Sea (Randall, 1983), are also important herbivores on coral reefs. No quantitative measures of abundance of siganids were made during this survey. However, these fish were much more abundant on

reefs in the south than in the central & northern Red Sea. On a swim along a 100m section of the fore-reef of a fringing reef in the central & northern Red Sea there were typically around 10-20 individuals at most but over a similar section of a reef in the south there were some 100-300 individuals. In addition, whilst only two species were routinely observed on central & northern reefs, all four species were commonly observed on southern reefs. Quantitative data on the distribution of siganids are clearly required before a firm conclusion can be drawn, but qualitatively the patterns of species richness and abundance of this family in the Red Sea support Russ's (1984a) findings. Interestingly, whilst the abundance and species richness of surgeonfish and parrotfish were broadly correlated with primary productivity in Russ's study, those of siganids did not. However, it is quite possible that Russ's (1984a) conclusion about the effects of productivity was spurious. There are many other changes, particularly in habitat, over the region studied by Russ (Done, 1982) which may be of more significance.

Patterns of species richness in surgeonfish and parrotfish from north to south within the Red Sea are similar to those found for damselfish (Roberts and Ormond, in prep.) with there being more species overall in central & northern regions than in the south. In addition to the suggested effects of productivity differences (Russ, 1984a), this is the opposite of what is expected on two other counts. The first is that in most animal and plant communities species richness declines with increasing latitude (Pianka, 1966), and the second is the 'peninsula effect'. Species richness often declines towards the extremities of a peninsula (MacArthur and Wilson, 1967; but see Busack and Hedges, 1984) and the Red Sea is effectively a peninsula of the Indian Ocean. Habitat changes between central & northern and southern regions probably account for much of the observed patterns, as suggested for damselfish (Roberts and Ormond, in prep.). Habitat heterogeneity is greater in the former than the latter regions, southern Red Sea fringing reefs lacking the deep fore-reef and well-developed lagoon zones typical of central & northern reefs. Sheppard and Sheppard (1985) identified thirteen distinctive coral assemblages in the central Red Sea compared with only six in the south (Sheppard, 1985). The absence of the deep fore-reef zone may at least partially explain the absence of surgeonfish species of the genus Naso from inshore reefs in the south. These species are usually found during the day in large shoals at depths of between 5 and 40m on reefs in the central & northern Red Sea.

That the habitat changes between central & northern and southern regions of the Red Sea have a major influence on the fish fauna occupying these regions is shown clearly in the cluster analyses of sites based on surgeonfish and parrotfish species presence/absence data. Surgeonfish communities inhabiting southern reefs are very distinct from those on central & northern reefs. This division is not

quite as clear-cut for parrotfish but is still obvious. Damselfish communities show a similar abrupt change around the same point within the Red Sea (Roberts and Ormond, in prep.). At a smaller scale, within the southern Red Sea, communities of surgeonfish inhabiting 'turbid' and 'algal' reefs differ predictably from those inhabiting 'clearwater' and 'classic' fringing reefs. Again, parrotfish communities are less distinct than surgeonfish communities but do show similar patterns. Parrotfish appear to be more generalist in the habitats they occupy than surgeonfish. Randall and Ormond (1978) suggested that it was the generalist feeding habits of Scarus ferrugineus which accounted for its very broad distribution within reefs. This is also reflected at a larger scale, S. ferrugineus being the most widely distributed of all the species observed in this study. Overall, compared with damselfish species, which in many cases have restricted ranges along the Saudi Arabian coast (Roberts and Ormond, in prep.), surgeonfish and parrotfish are much more widely distributed. However, this study shows that community structure of assemblages of parrotfish and surgeonfish species is strongly affected by the reef environment in which they live and that within the Red Sea, habitat factors have a more direct influence on their distribution than the effects of latitude, productivity, or isolation from the Indian Ocean source fauna.

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Chapter 3

Vertical zonation and habitat specificity of Red Sea damselfish (Pisces: Pomacentridae).

ABSTRACT

In this study we describe the vertical zonation patterns of damselfish on fringing reefs in the Saudi Arabian Red Sea with the aims of: (1) assessing the degree of habitat specialisation shown by damselfish at large and small scales, and (2) looking at spatial and temporal consistency of zonation patterns. Fish were counted by visual census along 200 x 5m transects laid at ten different depths at one site and at four depths at a further five sites. These sites were spread over a distance of approximately 850km throughout the central & northern Red Sea and were chosen for comparability of reef structure. At two sites, fish were counted yearly for three years (1982-1984). Small scale habitat specialisation was investigated by characterising the microhabitats occupied by damselfish species inhabiting the same reef zones. Distributional overlap between species is related to feeding guild. Species most dependent on the substratum for food and reproduction (territorial herbivores) overlapped least in distribution, whilst species which depend on the substratum only for shelter (planktivores) overlapped extensively in distribution. Omnivores fall somewhere between these guilds in extent of distributional overlap between species. These guild-related differences in habitat differentiation between species were also apparent in within-zone differences in microhabitat. Zonation patterns of most species were qualitatively largely consistent between sites and between years (within sites) despite sometimes large differences in absolute abundance.

INTRODUCTION

Wherever an environmental gradient exists, the animals and plants which occupy that environment usually have discontinuous ranges, each species only inhabiting a part of the total area (Pielou, 1975). For example, patterns of distribution of intertidal organisms (Underwood and Denley, 1984), distributions of bird species on mountainsides (Diamond, 1973) and trees in mangrove forests (Cragg, 1983). Coral reefs are an environment in which there are many changes in physico-chemical conditions moving from shallow to deep water. On fringing reefs, for example, the shallowest parts are usually tidal and subject to periodic exposure; wave action decreases from shallow to deep water; light intensity decreases with depth and light quality changes with depth; rates of sediment deposition are higher towards the shore and in deeper water than at the edge of the reef, etc. (Huston, 1985).

There are few, if any, cosmopolitan species of animals or plants which can thrive equally throughout the whole of this spectrum of conditions. Coral reefs typically have many recognisable zones with characteristic morphologies and compositions of coral species (Done, 1983; Sheppard, 1980). These arise from a complex interaction between physical factors, primarily wave action and light, and the animal (primarily coral) and plant species which inhabit them. Interactions between species are also important (Lang, 1973; Sheppard, 1982; but see Bradbury and Young, 1981). Zones may be defined primarily by their structure (e.g. spur-and-groove zone) or by dominant species (e.g. Acropora cervicornis zone of some Caribbean reefs; Alevizon et al., 1985).

The physical structure of the substratum has been shown to have a considerable influence on the diversity and abundance of fishes on coral reefs (Risk, 1972; Luckhurst and Luckhurst, 1978; Gladfelter and Gladfelter, 1978; Carpenter et al., 1981; Roberts and Ormond, in prep. a). However, fishes may in turn affect the structure of the substratum, primarily through algal grazing (Brock, 1979) and patterns of territoriality (Dart, 1972; Vine, 1974; Wellington, 1982; Roberts, 1985). Fishes may also have highly specific habitat requirements which can to a large extent determine their distribution. For example, anemonefishes are dependent on stochactid anemones for protection (Allen, 1972). Likewise, some species of goby and damselfish will only inhabit one or a few species of coral (Tyler, 1971; Sweatman 1983). As with corals, the distribution of fishes is thus a result of a complex interaction of abiotic and biotic influences.

The distribution and zonation of fish communities on coral reefs has attracted much study (e.g. Gosline, 1965; Bradbury and Goeden, 1974; Clarke, 1977; Harmelin-Vivien, 1977; Bouchon-Navaro, 1980; Bouchon-Navaro and Harmelin-Vivien, 1981; Robertson and Lassig, 1980). However, almost all studies have restricted attention to the fish communities inhabiting only one site or several sites in close

proximity (but see Edwards and Rosewell, 1981 and Russ, 1984). This study looks in detail at the zonation patterns of damselfish (Pomacentridae) on a reef near Jeddah on the Saudi Arabian, Red Sea coast. In addition, five other sites, covering a distance of 850km to the north, were looked at (in somewhat less detail) allowing comparison of zonation patterns between reefs at a large scale. Damselfish were chosen for this study because this family has been the focus of much debate concerning the community structure of coral reef fish communities (Sale, 1974; 1979; Robertson and Lassig, 1980; Ebersole, 1985), and because they are diverse and abundant on coral reefs. We seek to assess how much damselfish species differ in their use of space on reefs, both at a large scale (vertical distributional ranges) and at a small scale (within-zone differences in microhabitat) where the ranges of ecologically similar species overlap. The extent to which differences in spatial resource use contribute to coexistence between damselfish is discussed.

METHODS AND STUDY AREA

The study area

This study was conducted on fringing reefs of the central and northern part of the Saudi Arabian Red Sea coast, during the years 1982 - 1984 (Figure 1). Fringing reefs in this region of the Red Sea are typically well-developed and drop steeply into deep, clear water (Ormond *et al.*, 1984; 1986; Sheppard and Sheppard, 1985). Figure 2 shows the characteristic profile of such a reef. Whilst fringing reef structure throughout the study area is relatively uniform, and sites were chosen for comparability of structure, physico-chemical conditions vary considerably (Morcos, 1970). Most importantly, there are gradients in salinity, surface temperature and tidal amplitude throughout this region and these are considered in more detail elsewhere (Roberts and Ormond, in prep. b;c). These parameters may have important influences on damselfish community composition and possibly zonation patterns (Roberts and Ormond, in prep. a).

Study species

Damselfish are abundant and ubiquitous on coral reefs throughout the tropics (Allen, 1975). Thirty-four species are known from the Red Sea and these are described in Allen and Randall (1980). Of these, twenty-seven species were observed during this study and were identified according to Allen and Randall (1980) and Randall (1983). All are easily recognisable underwater and can be identified unambiguously. Species are referred to by the names used in Randall (1983).

Fish censusing procedure

At a site near Jeddah, individuals of all species of damselfish were counted by visual census along ten, 200m transects with estimated widths of 5m, laid from 0.5m deep in the lagoon to 24m deep on the fore-reef slope (Figure 2). Transects were laid parallel to the reef crest. At five other sites to the north of Jeddah (Ras Hatiba, Rabigh, Ras Baridi, Al Wadj and Tiran, Figure 1), four 200 x 5m transects were laid on the fore-reef at depths of 1m, 1.5m, 6m and 12m. These depths correspond to recognisable reef zones: 1m terrace (1m), reef-edge (1.5m), reef-face (6m), and fore-reef slope (12m). They are directly comparable to four of the Jeddah transects. Three replicate counts were made along each of the Jeddah transects whilst only one count was made along each transect at the other locations. All counts were made by the senior author to eliminate inter-observer variability.

Reefs at all sites were very similar in structure (see Figure 2)

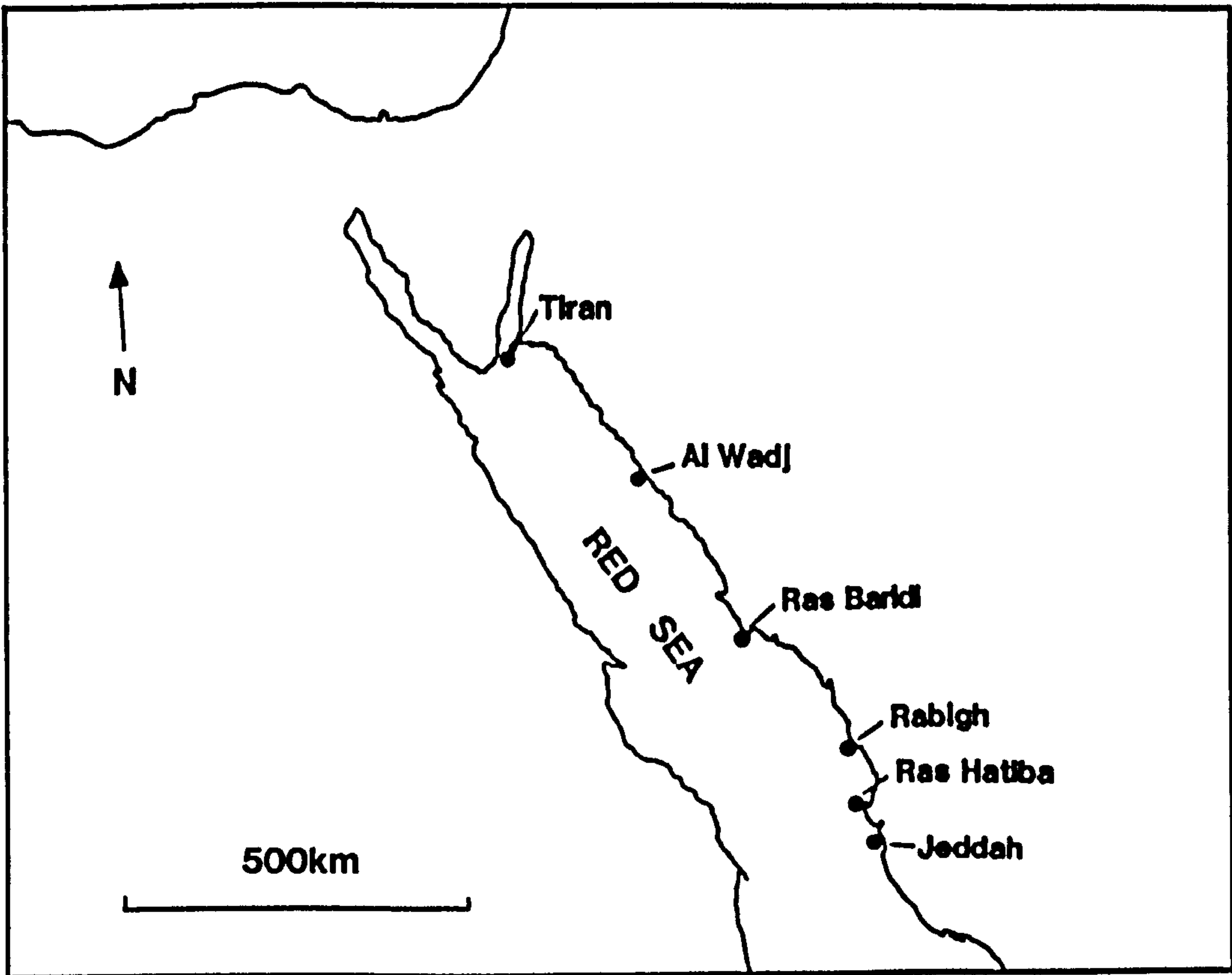


Figure 1: Map of the northern Red Sea showing the locations of the study sites.

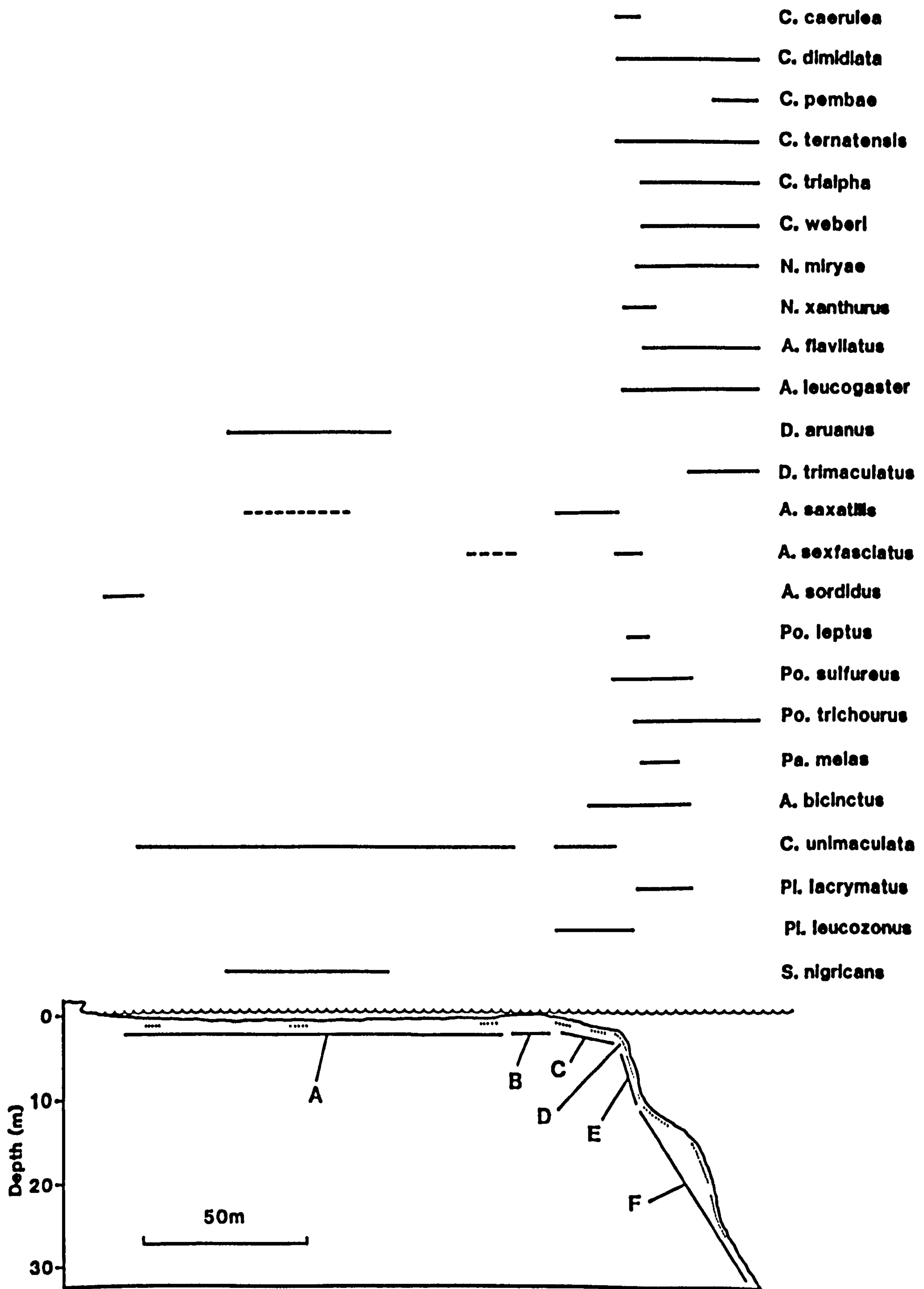


Figure 2: Zonation patterns of damselfish species over the reef at the Jeddah north site. Dashed lines indicate parts of the reef inhabited only by juveniles of the species. Dotted lines show the locations of the ten 200 x 5m transects. Zones of the reef are: (A) lagoon, (B) reef crest, (C) 1m terrace, (D) reef-edge, (E) reef-face, and (F) fore-reef slope.

except that shallow regions of reefs in the north (Ras Baridi, Al Wadj and Tiran) have a different structure from those further south, due probably to the increasing tidal amplitude from the central to the northern regions of the Red Sea. These reefs lack a distinct reef crest and lagoon zone, and water in the 1m terrace/reef-flat zone typically becomes very shallow (< 0.3m deep) at low tide (Roberts and Ormond in prep. b).

Accuracy of visual census technique

Visual census techniques allow fish in large areas of reef to be counted quickly and non-destructively. They have been widely used and have been found to be an acceptably accurate method of counting diurnal, non-cryptic species (Brock, 1982; Harmelin-Vivien et al., 1985; but see Sale and Sharp, 1983). All species of Red Sea damselfish are diurnal and non-cryptic, although one, Pomacentrus leptus, is rather secretive in its habits. In this and most other surveys employing visual census (e.g. Ehrlich et al., 1977; Robertson and Lassig, 1980; Anderson et al., 1981), transect width has been visually estimated. In order to determine the sampling variance due to visual estimation of transect width, a 200m transect was set up at 1.5m depth on the reef-edge of a reef near Jeddah. Over 100m of this the width was marked using fixed lines 5m apart. The other 100m was left unmarked and transect width visually estimated. Five counts of damselfish along each section were made on each of two consecutive days. Counts for each species were not totalled until all counts were completed to minimise observer bias. These data allow an assessment of between-count variability, and variability due to visual estimation of transect width. Kendall's tau rank correlation coefficients were calculated between all pairs of counts for both marked and unmarked transects.

Year-to-year variability

Counts of damselfish were made along the four fixed transects at the Jeddah site (1m, 1.5m, 6m and 12m) in the period July to September in 1982, 1983 and 1984. A second site at Jeddah was also censused in this way. These data make possible an assessment of between-year changes in damselfish community composition and variability in vertical distribution patterns. The percentage similarity index (PSC) was used to assess between-year change in community composition (numbers of individuals of each species on all four transects pooled) and is calculated as follows:

$$\text{PSC} = 100 - 0.5 \sum |a - b|$$

where a and b are, for a given species, percentages of the total samples A and B represented by that species (Washington, 1984). An estimate of year-to-year changes in zonation is obtained by calculating Kendall's tau rank correlation coefficients between years, keeping counts of species from each transect separate.

Distinctiveness of damselfish communities from different reef zones

In addition to descriptive treatment of damselfish zonations at each site on an individual species basis, the composition of damselfish communities occupying each of the four zones censused is looked at using principal components analysis. Principal components analysis allows a description of between-site differences in community composition within each zone, and thus of the distinctiveness of these zones in terms of their resident damselfish communities.

Microhabitat characteristics

Whilst the vertical distributions of many damselfish species may overlap considerably on Red Sea reefs, this does not necessarily mean that these species have the same habitat requirements. Two species occupying the same part of the reef may differ in the microhabitats which they occupy. To quantify microhabitats, the cover of different substrate types (Table 1) was estimated along two, two metre long transects laid perpendicular to each other and crossed at the centre, by recording the number of centimetres of line covering each type (converted to percentages). Each site was centred on the area corresponding to the approximate centre of home-range of the individual(s) under study. Ten sites were characterised in this way in each reef zone for individuals of fourteen species. The data are analysed using principal components analysis, performed separately for each reef zone.

Live hard coral:	9. Algal covered dead coral
1. Branching	10. Coral rock/coralline algae
2. Tabular	11. Filamentous algal lawn
3. Plate	12. Rubble
4. Encrusting	13. Algal covered rubble
5. Massive	14. Macro-algae
6. Complex massive*	15. Sand
7. Soft coral	
8. Dead coral	

Table 1: Substrate types distinguished in the micro-habitat characterisation study. * Complex massive colonies were distinguished from massive colonies as having a more convoluted form which affords greater cover to fish.

RESULTS

Accuracy of visual census technique

Kendall's tau correlation coefficients were calculated between all pairs of counts made along the 100 x 5m transects with the width marked and unmarked. Counts on which transect width was marked had a median correlation coefficient of 0.91 with a range of 0.73 - 0.99. Counts on which transect width was visually estimated had a median correlation coefficient of 0.81 with a range of 0.68 - 0.96. It is clear that visual estimation of transect width does impair the accuracy of the method. However, with a median correlation of 0.81, we feel that the accuracy of counting fish on unmarked transects is sufficiently good for the purposes of this study.

The composition of the damselfish communities in the two adjacent 100 x 5m transects censused at this site was very similar, with a percent similarity index of 86.8%. This indicates that, although transects were not replicated at sites, single counts along 200 x 5m transects give a representative picture of damselfish zonation at each. It is unlikely that replicating transects within sites would significantly alter the results presented here.

Zonation patterns

Jeddah Figure 2 shows the vertical distributions of the twenty-four species of damselfish recorded from the Jeddah site. This has been compiled using the data from the ten 200 x 5m transects counted at this site (the locations of which are shown) and from several hundred hours of additional observations at this site during 1982 - 1984. All species have discontinuous ranges and many have very restricted distributions.

Figure 3 shows a quantitative breakdown by guild of the distributions of the commoner species at this site. Three feeding guilds are defined: planktivores, omnivores and territorial herbivores. Planktivorous damselfish are those which feed almost exclusively on plankton, whilst omnivorous species may also feed extensively on plankton but will feed on benthic invertebrates and algae too (usually algae only constituting a small proportion of the diet [Fishelson et al., 1974]). Territorial herbivores hold interspecifically defended territories against most other herbivorous and some omnivorous species. Filamentous algae constitute the bulk of their diet but benthic invertebrates and plankton are sometimes taken (Roberts, 1985). Figure 3a shows the distributions of the four species of territorial herbivore. Chrysiptera unimaculata is primarily found in the lagoon and back-reef zones but is also found in considerable numbers on the 1m terrace. Stegastes nigricans is very uncommon at this site and is restricted to small reef patches in the deeper parts

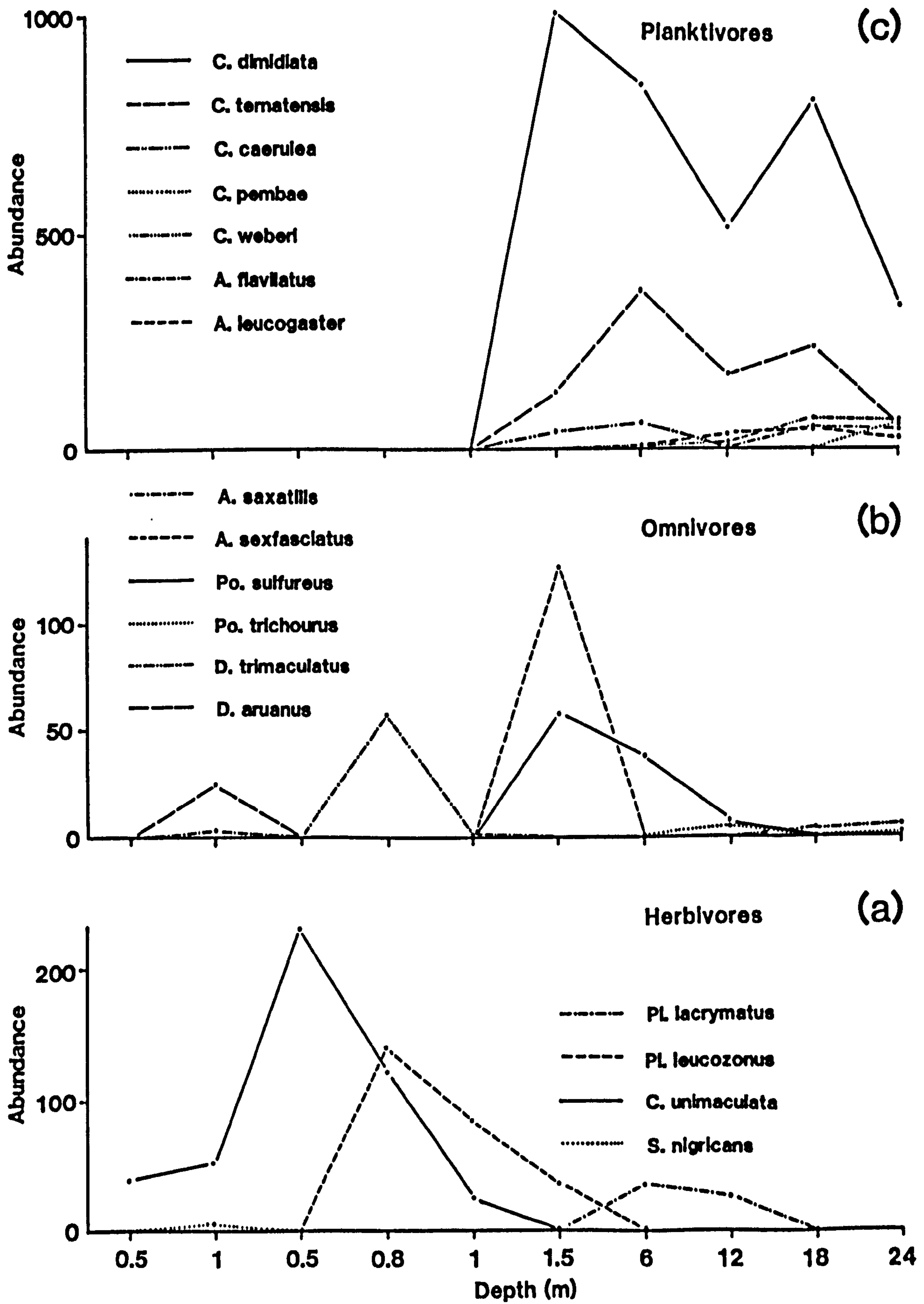


Figure 3: Quantitative distributions of species over the reef at the Jeddah north site; from counts along the ten 200 x 5m transects (Figure 2). Note that scales differ between graphs.

of the lagoon. Plectroglyphidodon leucozonus is only found on the 1m terrace and Pl. lacrymatus is restricted to the fore-reef slope (although occasional small juveniles are found on the 1m terrace). There is thus substantial habitat differentiation between these species.

Figure 3b shows the distributions of omnivorous species. These come from three genera: Abudefduf, Dascyllus and Pomacentrus. The distributions of all three pairs of congeneric species overlap very little or not at all. Dascyllus aruanus inhabits colonies of branching corals (primarily Stylophora pistillata) in the deeper parts of the lagoon, whereas D. trimaculatus is found only on the fore-reef, usually in the deeper regions. Juveniles of the latter species are often found in association with stoichactid anemones. Abudefduf saxatilis occupies the shallow waters towards the rear (reef crest) part of the 1m terrace. A. sexfasciatus is found almost exclusively at the reef-edge although juveniles of both these species are found in the lagoon. A. sordidus, the only other member of this genus found in the Red Sea, inhabits the rocky-rubble shoreward fringe of the lagoon (Figure 2) and was thus not observed on any transects. Pomacentrus sulfureus is most abundant at the reef-edge and over the reef-face. Po. trichourus is uncommon at this site and inhabits only the fore-reef slope. Observations at other sites in the central Red Sea indicate that this is its primary habitat. One other omnivorous species of Pomacentrus, Po. leptus, was observed at this site but was very uncommon. It was only observed on the 6m transect. Similarly two other omnivores, Amphiprion bicinctus (an anemonefish), and Paraglyphidodon melas were uncommon. The former species inhabits almost any part of the reef where there are stoichactid sea anemones (CR, personal observations; Fricke, 1977).

Planktivorous fishes (Figure 3c) are all confined to the fore-reef, from the reef-edge to the base of the fore-reef slope. Two species, Chromis dimidiata and C. ternatensis are abundant at Jeddah, and both inhabit the whole of the fore-reef. C. caerulea is found only in the shallower regions, at the reef-edge and on the reef-face. Three other species of Chromis, C. weberi, C. trialpha and C. pembrae all become increasingly common with increasing depth, the latter species only being found below 20m depth. The two species of Amblyglyphidodon have a similar distribution, although A. leucogaster is commoner in shallow water than A. flavilatus. Planktivorous damselfishes thus overlap extensively in their distributions. However, the abundance of the species over the fore-reef is not uniform. There are two pronounced peaks in abundance, the first between the reef-edge and the reef-face (1.5 and 6m) and the second at 18m. The reef at Jeddah has a 'stepped' structure (Figure 2) and these peaks correspond to the upper regions of the 'steps' and are structurally complex compared to other parts of the fore-reef (Roberts and Ormond, in prep. a).

Other sites Figures 4a-p show the comparative zonations of the sixteen commonest species of damselfish from six sites (Figure 1). Note that in order to illustrate zonation patterns clearly, each species is shown at a scale appropriate to its abundance. These Figures show high levels of between-site variation in abundance of all species. However, despite these differences in abundance, zonation patterns of many species are very similar between sites. The greatest levels of variability in zonation are apparent in three species of Chromis: C. caerulea, C. dimidiata and C. ternatensis. These species peak in abundance either at the reef-edge (1.5m) or on the reef-face (6m).

Zone specificity of damselfish communities

To assess how distinctive damselfish communities occupying the four zones censused were, a principal components analysis was run on counts from the six study sites. The results are shown in Figure 5. Each point represents one transect from one site. Non-overlap of data sets for transects at different depths is taken to mean that they have distinctive assemblages of damselfish (Nichols, 1977). The first two components, shown in Figure 5, account for 93% of the variance in the data and the plot is thus quite a precise representation of similarities and differences between transects at each site. The only zone which has a completely distinct damselfish assemblage is the 1m terrace. This zone is dominated almost exclusively by the territorial herbivores Chrysiptera unimaculata and Plectroglyphidodon leucozonus. Clusters of transects from 1.5, 6 and 12m all overlap to a large extent indicating that although these zones are distinguishable on the basis of their coral communities and morphology (G. Gaudian, pers. comm.), they have similar damselfish assemblages.

Year-to-year variability

Percent similarity indices were calculated between years using data from fixed transects (1, 1.5, 6, and 12m) at the two Jeddah sites, using the total abundance of each species (four transects pooled) at each site. This index gives an indication of the between-year changes in damselfish community composition, although not in absolute abundance. These are shown in Table 2. There is a high level of similarity between years at both sites. However, given the short timespan over which this study was conducted (two years) this is perhaps not surprising.

High between-year similarities may also arise due to the strong dominance of these communities by Chromis dimidiata and C. ternatensis, which will mask changes in the less common species. Excluding these species from calculations of PSC reduces the between-year similarities by an average of 16.3% (Table 2).

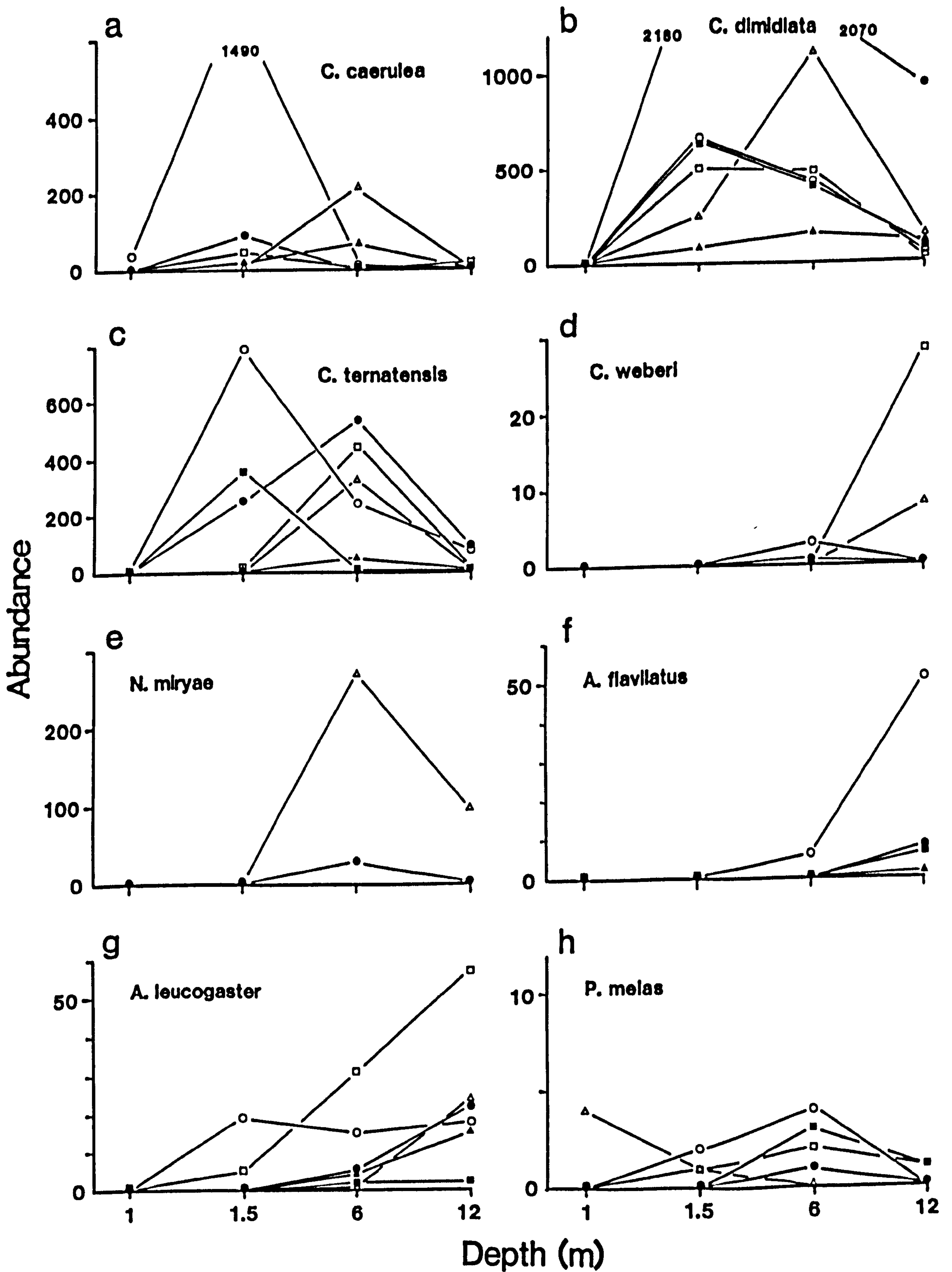


Figure 4: Zonation patterns of damselfish species from the six study sites: ● Jeddah north site, ○ Ras Hatiba, ■ Rabigh, □ Ras Baridi, ▲ Al Wadj, and △ Tiran. Where no points are shown for a site the species was not recorded. Note that scales differ between graphs.

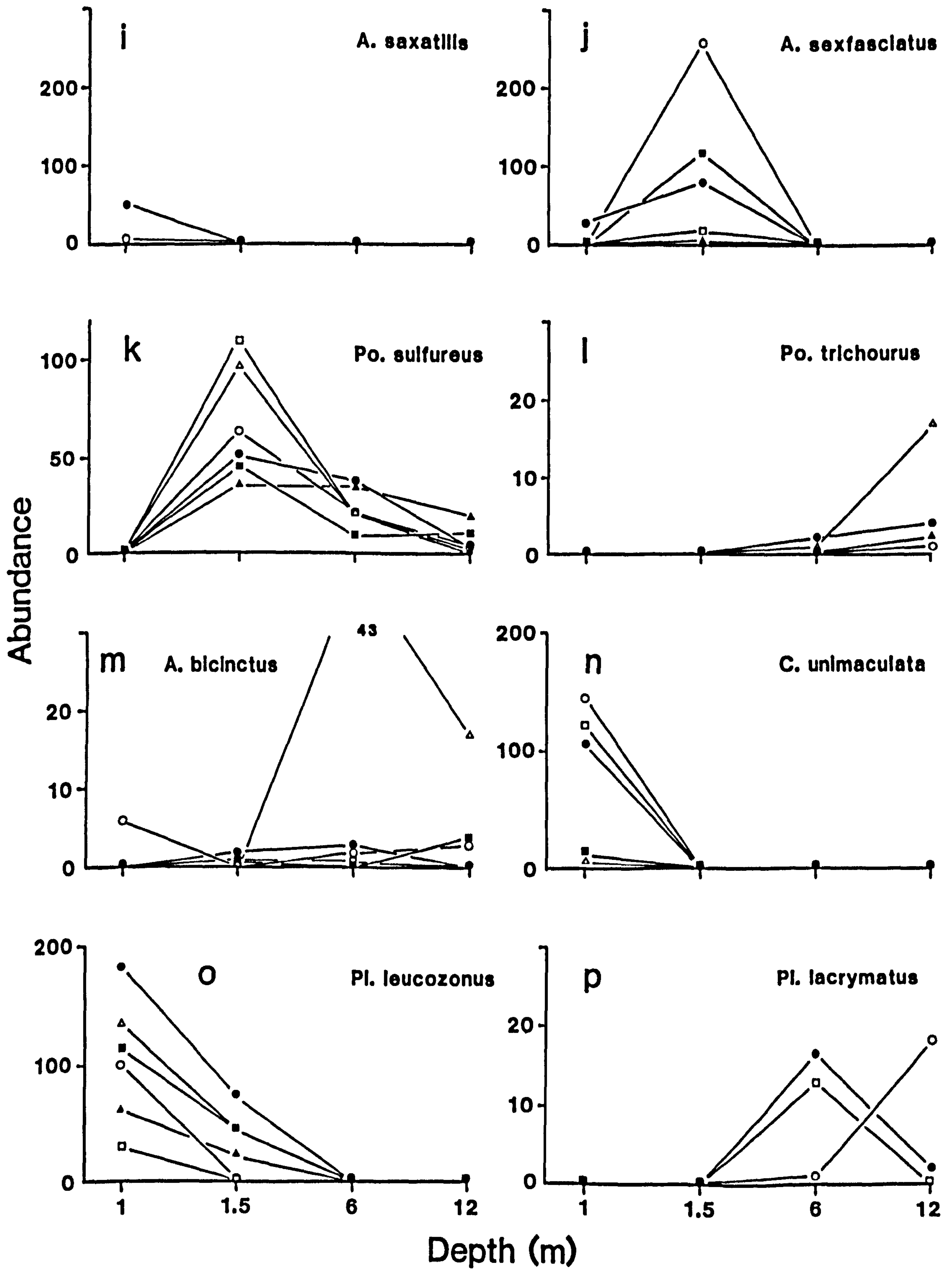


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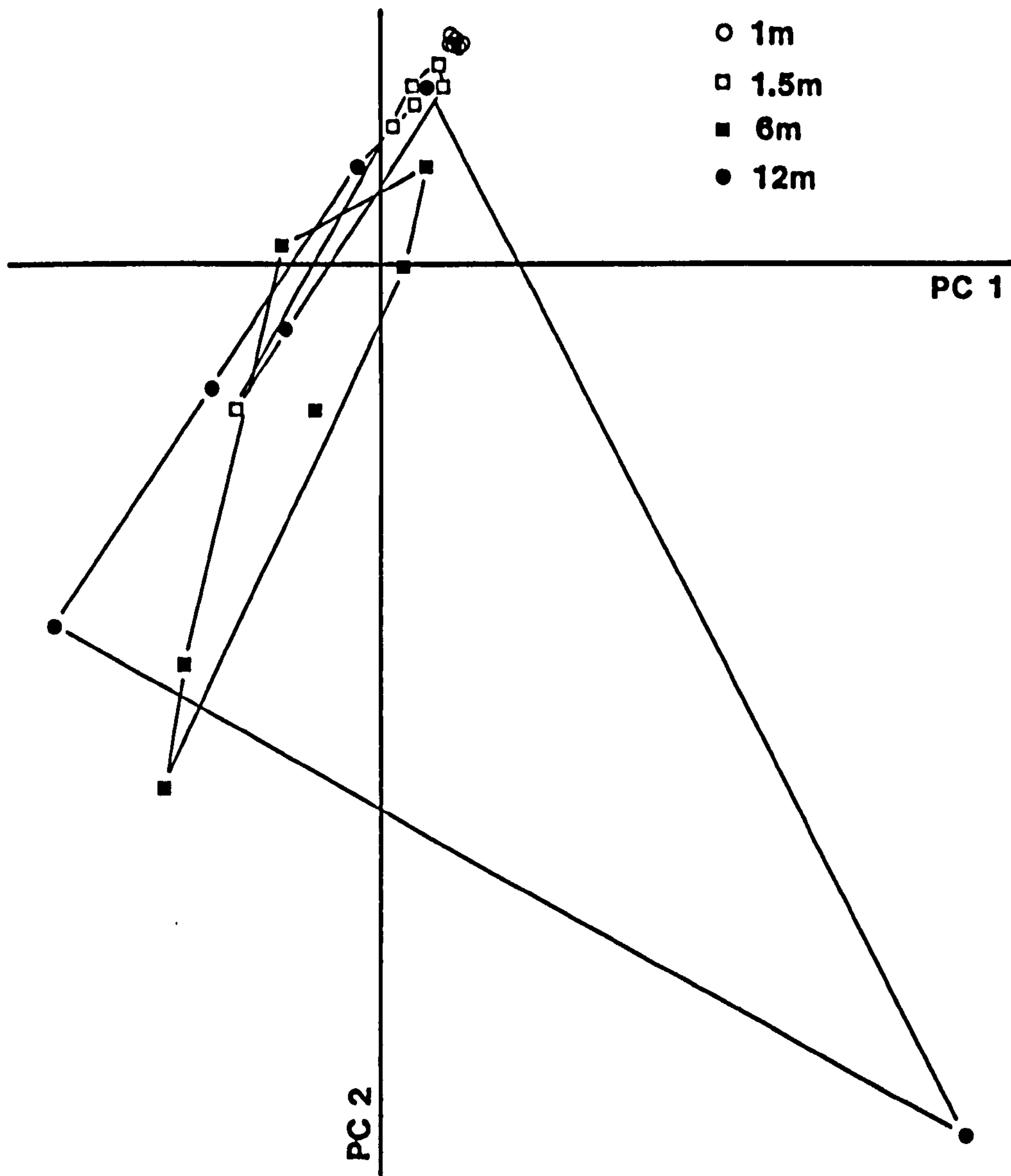


Figure 5: Principal component analysis of transect counts of damselfish from six sites. Components 1 and 2 account for 93.0% of the variance in the data. Each point represents one transect count at one site.

	<u>Jeddah North</u>		<u>Jeddah South</u>	
	A	B	A	B
1982 vs 1983	86.6	67.1	93.4	74.1
1983 vs 1984	84.0	72.6	93.1	76.8
1982 vs 1984	94.5	82.5	92.9	73.4

Table 2: Percent similarity indices for between-year comparisons of damselfish communities at two sites on the reef near Jeddah. A = all species; B = excluding the abundant schooling planktivores Chromis dimidiata and Chromis ternatensis.

Despite quite large changes between years in the abundance of some species, the patterns of abundance distribution over the reef remained virtually identical for nearly all species (Figures 6a-o and 7a-m).

Microhabitat segregation

Data on microhabitat characteristics (percent cover of different substrata within home-range; Table 1) for fourteen species of damselfish from three reef zones (lagoon, 1m terrace and reef-face/fore-reef slope) were analysed using principal components analysis. Analyses were run separately for species occupying each zone and the results are shown in Figures 8a-c. The method used to record microhabitat characteristics encompassed substrata within an area of 1m radius around the estimated 'central point' of the home-range of each damselfish. Hence this only represents an approximation of the microhabitat. Using this method, species occupying very different microhabitats may appear to be similar if these microhabitats usually only account for a small proportion of the area recorded. Table 3 shows the most abundant substrata within the home-ranges of individuals of each species in each reef zone.

Lagoon

Figure 8a shows that there is considerable separation between three lagoonal species in terms of microhabitat characteristics. These are Stegastes nigricans, Pomacentrus trilineatus and Chrysiptera annulata. Table 4 shows the important loadings of the substrate variables on the principal components, indicating which substrate characteristics contribute most to this separation. With the exception of Dascyllus aruanus, all the species studied in the lagoon are territorial herbivores. D. aruanus overlaps considerably in microhabitat with all of these species. However, it does not interact to any great extent with them since it is primarily a water column feeder (Sweatman, 1985a). Figure 8a suggests that the microhabitat of Chrysiptera unimaculata is less distinctive than those of the other herbivores but is still somewhat different from those occupied by these species.

1m terrace

Figure 8b shows the microhabitat separation between species inhabiting the 1m terrace zone, and Table 4 the important variable loadings on the principal components. Once again, four of the five species are territorial herbivores, the exception being Paraglyphidodon melas, a solitary omnivore. This latter species overlaps considerably in microhabitat characteristics with Pomacentrus

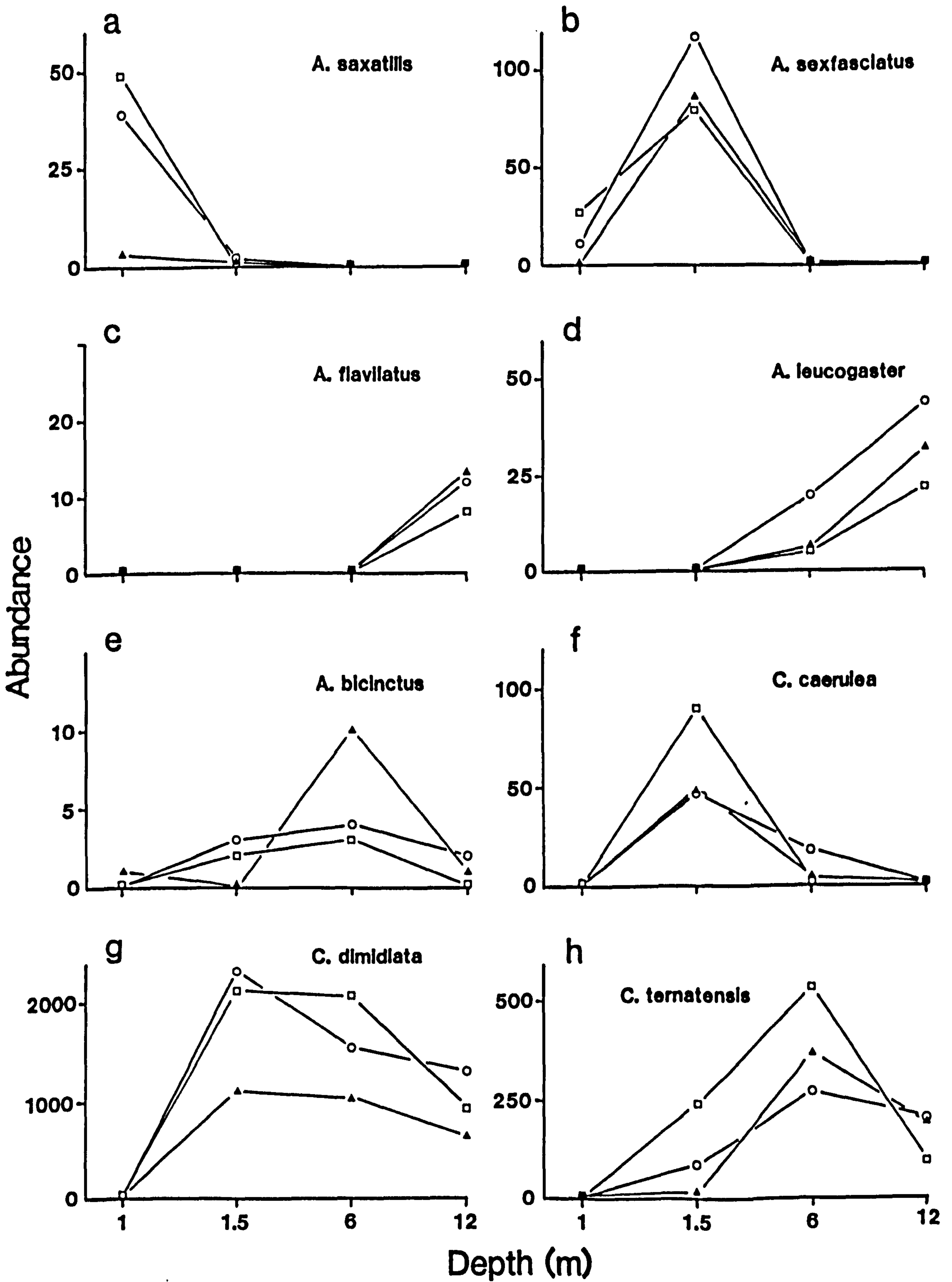


Figure 6: Year-to-year differences in the abundance distributions of damselfish species at the Jeddah north site: \square 1982, \blacktriangle 1983, and \circ 1984.

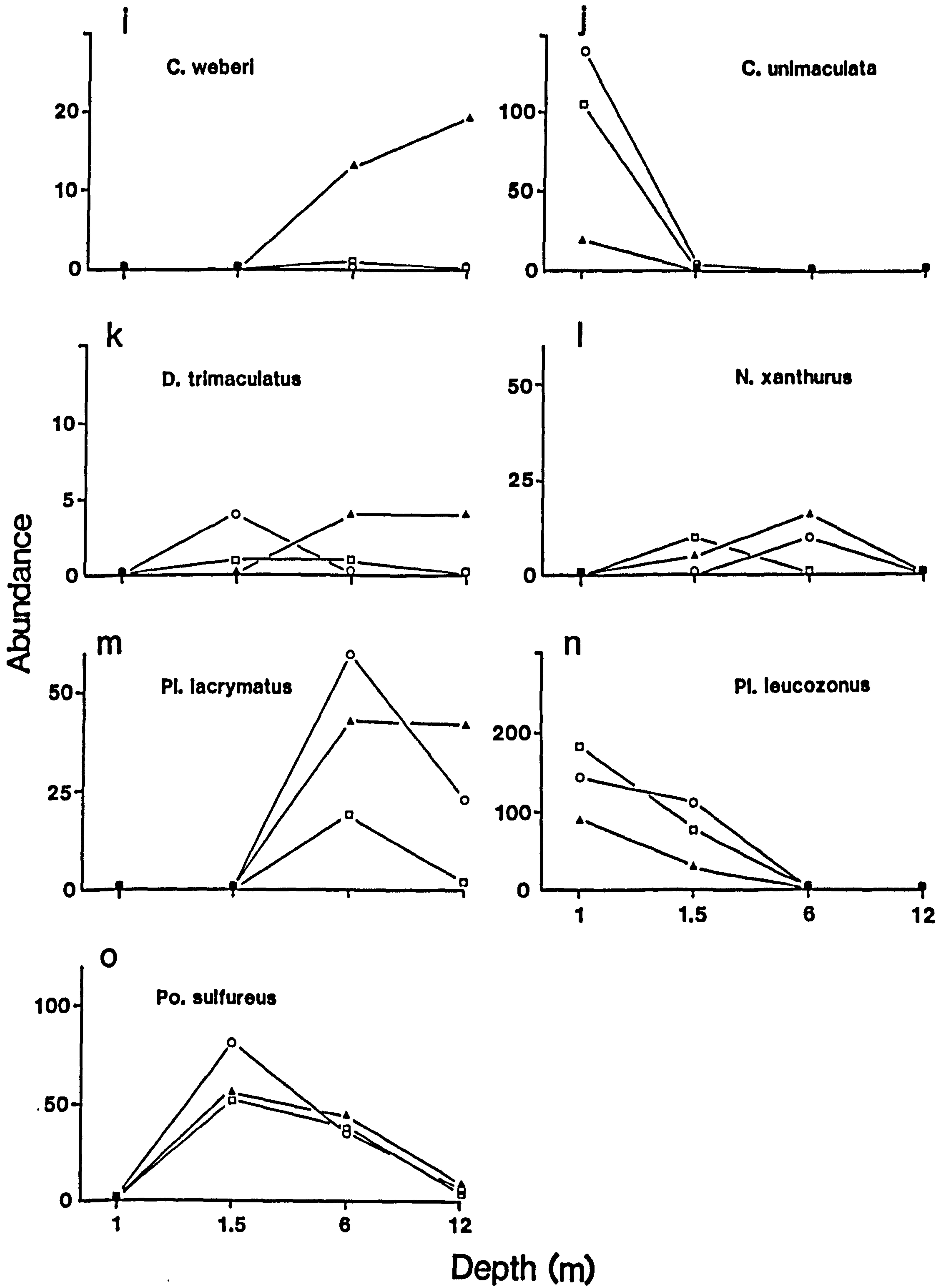


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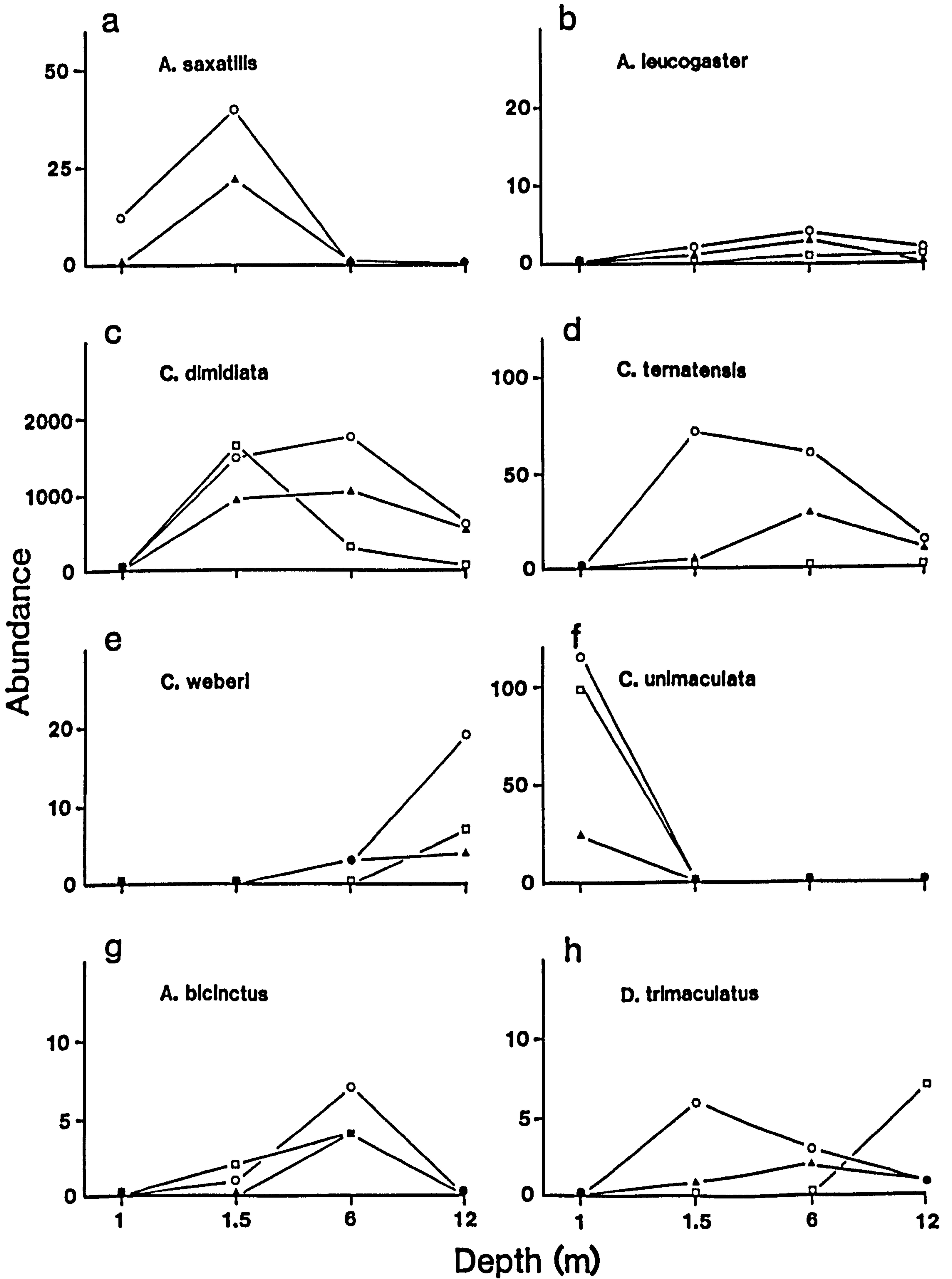


Figure 7: Year-to-year differences in the abundance distributions of damselfish species from the Jeddah south site: \square 1982, \blacktriangle 1983, and \circ 1984.

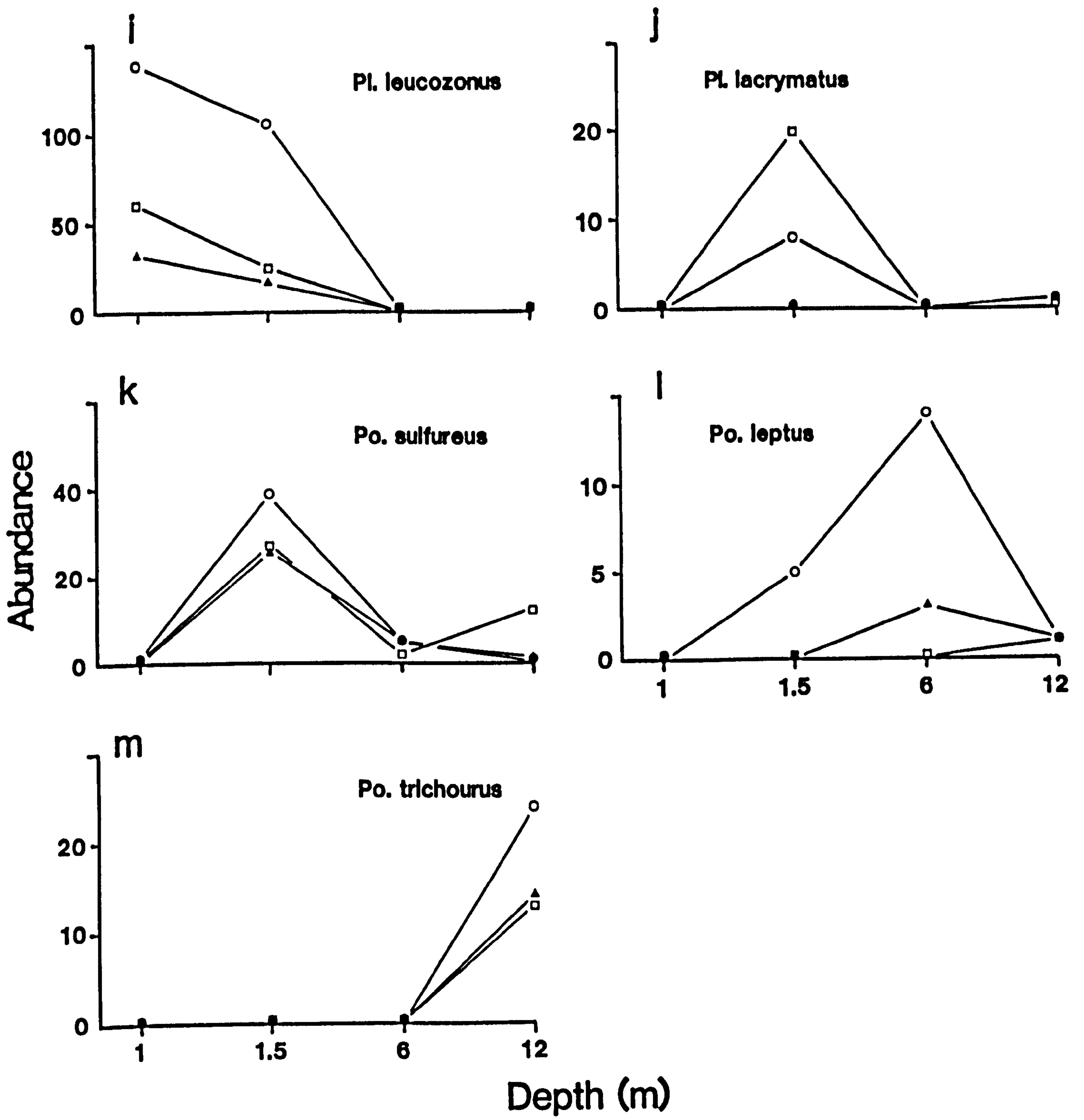


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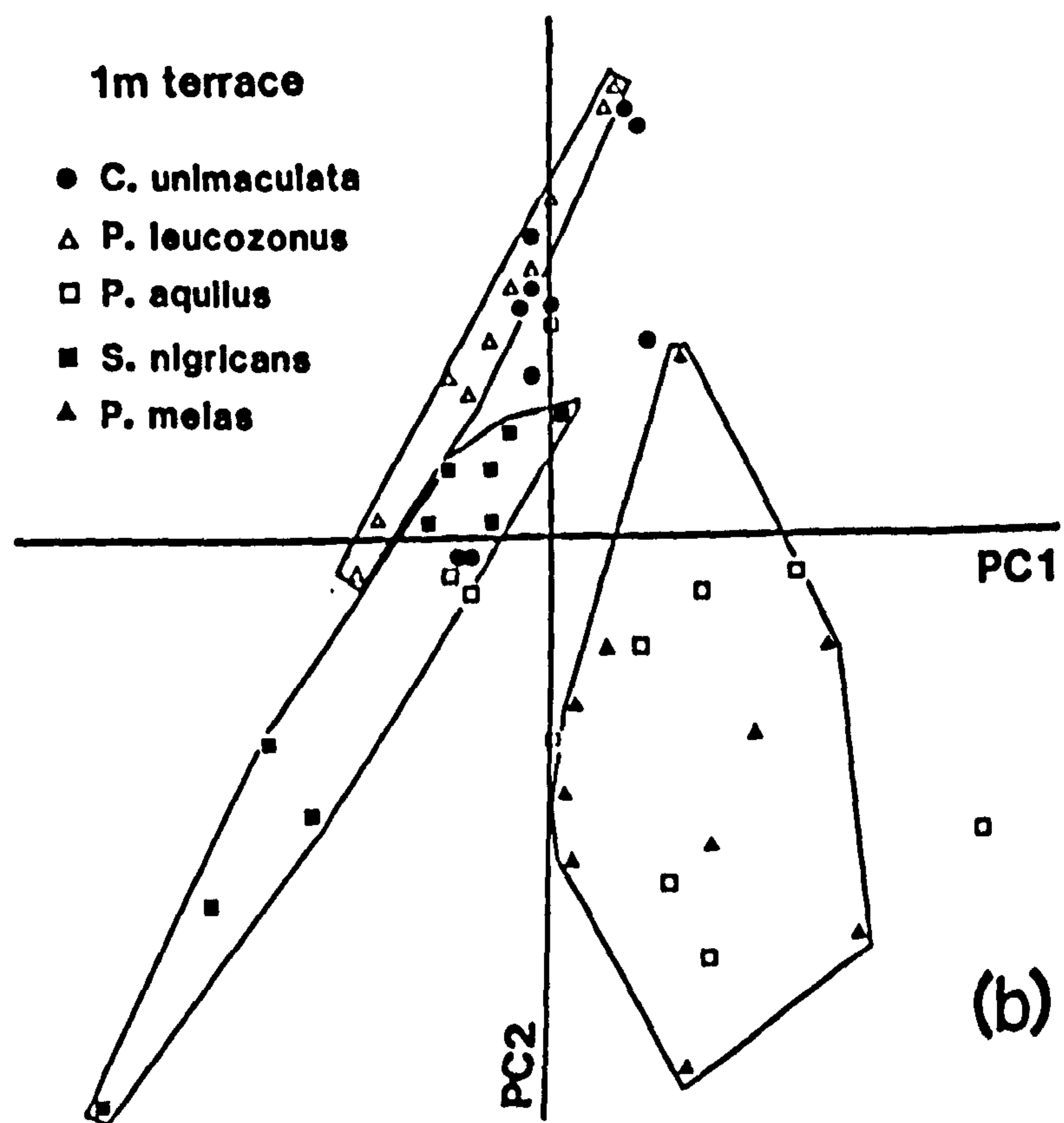
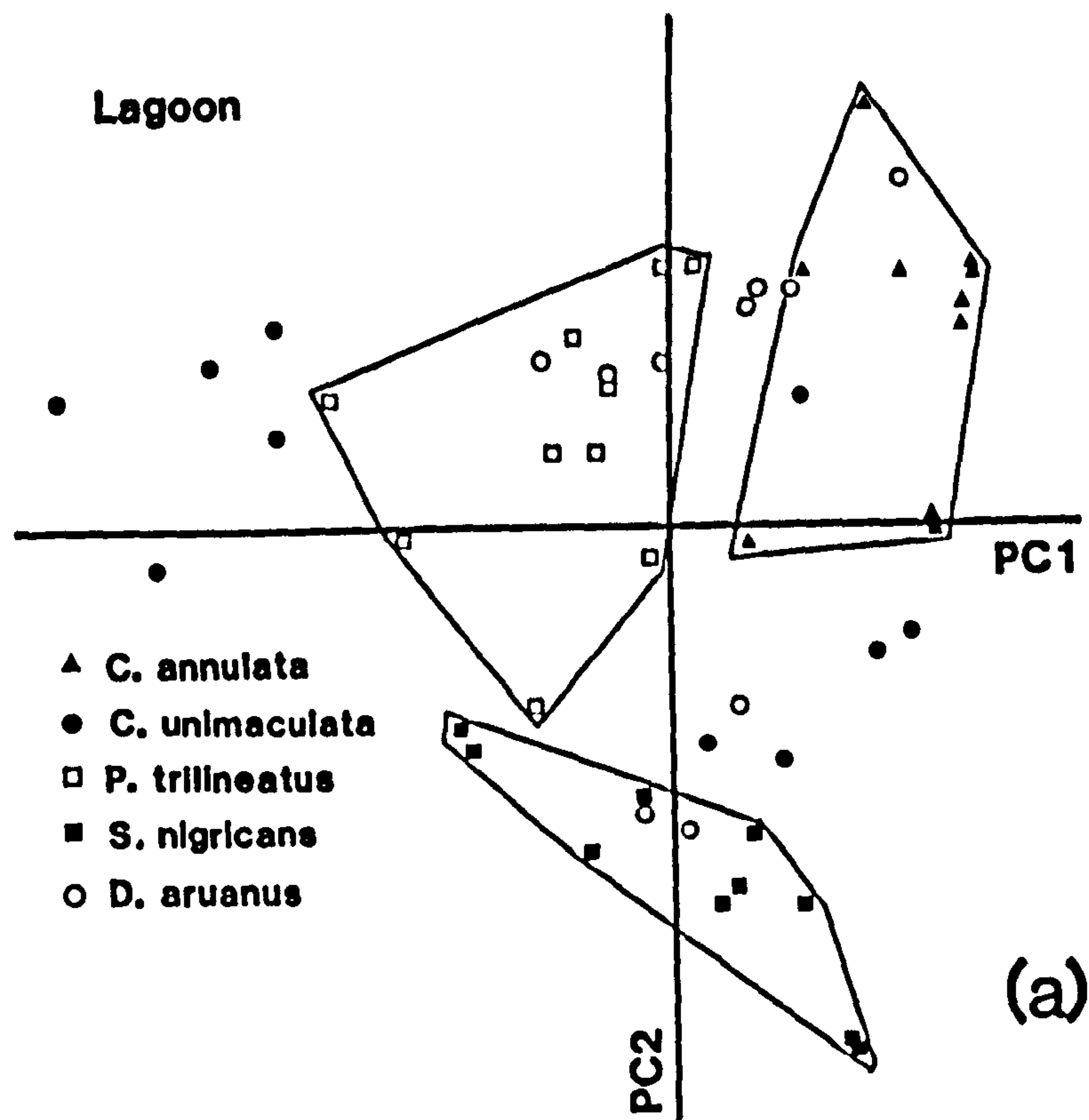


Figure 8: Principal component analyses of damselfish microhabitat characteristics. Components 1 and 2 account for: (a) 71.9% of the variance, (b) 74.4%, and (c) 66.1%. Discrete clusters are outlined.

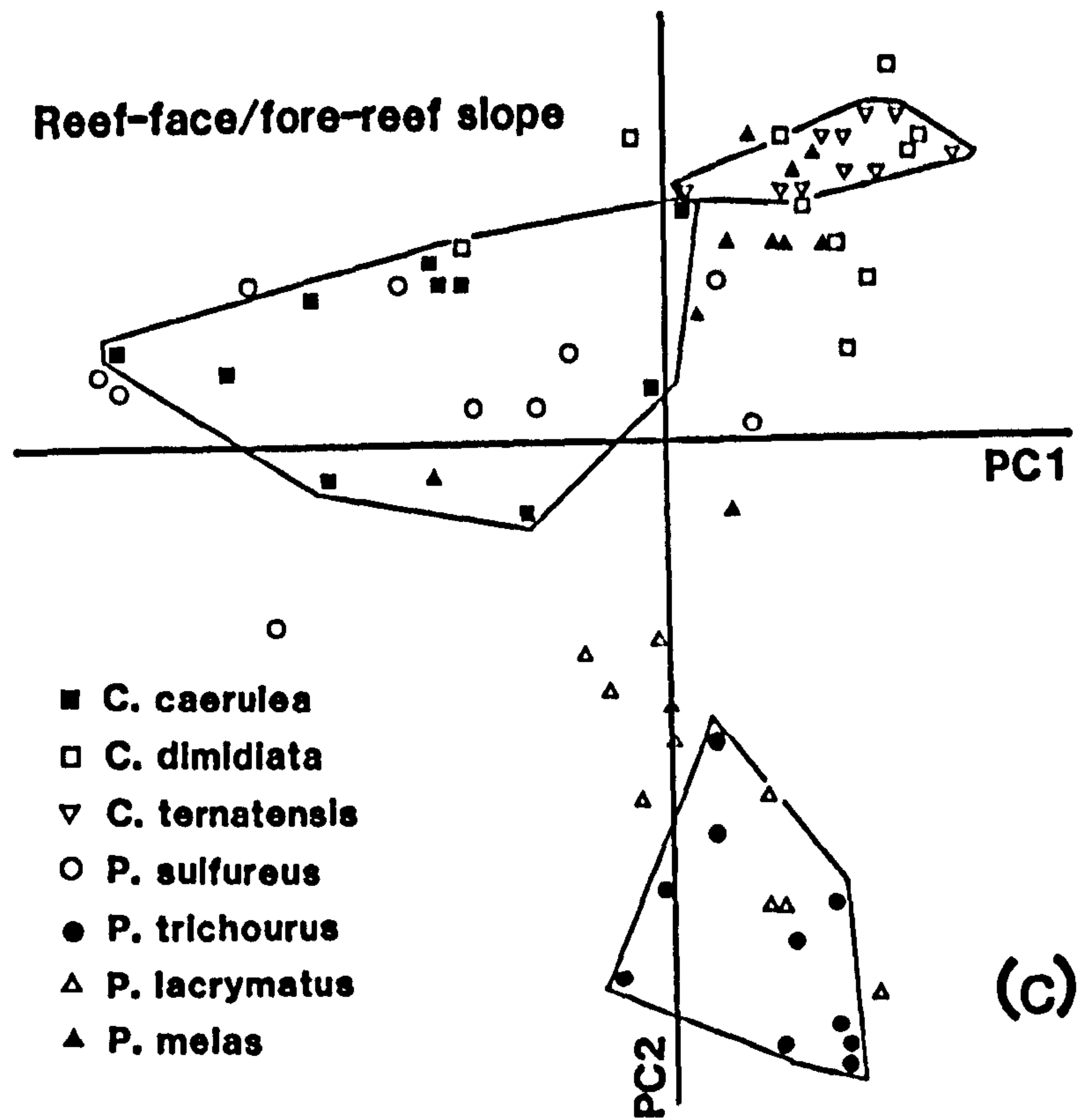


Figure 8: ...continued.

SPECIES	MEAN % COVER (+ S.E.)	DESCRIPTION
Lagoon		
<u>C. annulata</u>	65.5 + 4.7	Sand
	27.3 + 4.9	Filamentous algal lawn
<u>C. unimaculata</u>	30.6 + 8.6	Filamentous algal lawn
	27.3 + 4.6	Sand
	22.6 + 8.1	Macro-algae
<u>D. aruanus</u>	38.5 + 7.7	Sand
	25.4 + 7.6	Filamentous algal lawn
	21.1 + 1.4	Branching coral
<u>P. trilineatus</u>	32.8 + 5.1	Sand
	20.7 + 5.2	Filamentous algal lawn
<u>S. nigricans</u>	72.0 + 6.2	Filamentous algal lawn
1m terrace		
<u>C. unimaculata</u>	74.2 + 4.1	Filamentous algal lawn
<u>P. melas</u>	45.0 + 4.4	Filamentous algal lawn
	24.4 + 3.5	Coral rock/coralline algae
<u>P. leucozonus</u>	75.2 + 4.1	Filamentous algal lawn
<u>P. aquilus</u>	53.2 + 3.9	Filamentous algal lawn
	21.1 + 4.5	Coral rock/coralline algae
<u>S. nigricans</u>	46.3 + 4.4	Filamentous algal lawn
Reef-face/fore-reef slope		
<u>C. caerulea</u>	45.9 + 5.9	Branching coral
	22.5 + 3.2	Coral rock/coralline algae
<u>C. dimidiata</u>	34.8 + 5.3	Soft coral
	34.7 + 4.6	Coral rock/coralline algae
<u>C. ternatensis</u>	39.1 + 4.0	Soft coral
	36.5 + 2.8	Coral rock/coralline algae
<u>P. melas</u>	39.4 + 5.3	Coral rock/coralline algae
<u>P. lacrymatus</u>	25.7 + 7.6	Filamentous algal lawn
<u>P. sulfureus</u>	44.9 + 8.2	Branching coral
<u>P. trichourus</u>	46.6 + 4.4	Filamentous algal lawn
	25.2 + 3.9	Sand

Table 3: Dominant substrata and the average percentage cover of these within the microhabitats of each species within each reef zone.

SUBSTRATE TYPE	COMPONENT 1	COMPONENT 2
Lagoon		
Algal covered rubble	0.64	0.63
Filamentous algal lawn	-0.77	0.48
Algal covered dead coral	-	-0.28
Macro-algae	-	-0.48
1m terrace		
Filamentous algal lawn	0.86	-
Coral rock/coralline algae	-0.33	-0.40
Algal covered dead coral	-0.39	0.84
Reef-face/fore-reef slope		
Algal covered rubble	0.27	-
Filamentous algal lawn	-0.65	-
Algal covered dead coral	0.53	-
Soft coral	0.40	0.38
Live branching coral	-	-0.88

Table 4: Loadings of substrate variables on the principal components. Only loadings greater than 0.25 or less than -0.25 are shown. These loadings are equivalent to correlation coefficients.

aquilus. These species are unlikely to compete since P. melas is primarily a feeder on soft corals and suspended particulate matter (Randall, 1983). They occupy microhabitats which differ from the other species in this analysis. Stegastes nigricans and Plectroglyphidodon leucozonus also occupy relatively distinct microhabitats. Microhabitat characteristics of C. unimaculata overlap somewhat with those of Pl. leucozonus. However, Roberts (1985) has shown that in this zone they tend to occupy different areas, Pl. leucozonus dominating over C. unimaculata in areas inhabited by the territorial, herbivorous surgeonfish Acanthurus sohal.

Reef-face/fore-reef slope

Two species in this analysis occupy very distinct microhabitats from the other five although they overlap extensively with each other (Figure 8c). These are Pl. lacrymatus and Po. trichourus. The former, a colonial, territorial omnivore inhabits rubble patches on the fore-reef slope and the latter is a solitary omnivore which feeds primarily in the water column. Hence they are unlikely to interact significantly. Two species of planktivore, C. dimidiata and C. ternatensis, overlap extensively with each other and with the solitary omnivore P. melas. The microhabitats of these species are however somewhat different from that of another planktivore, C. caerulea and the omnivore Pomacentrus sulfureus. These latter species are most common in the coral rich regions of the reef-edge and the reef-face. The important loadings of substrate types on the principal components are shown in Table 4.

DISCUSSION

This study shows that amongst damselfish species in the Red Sea there is marked spatial partitioning of the reef environment. However, the degree to which species differ in patterns of space use differs between guilds. Three feeding guilds have been defined: planktivores, omnivores and territorial herbivores. It is this latter guild in which spatial differentiation in habitat use is most pronounced, both at the large scale of zonation within the reef and at the smaller scale of within-zone differences in microhabitat use. Substantial differences in vertical distribution were also found between omnivorous species. In contrast, there was little differentiation in zonation patterns or microhabitat use between planktivorous damselfish. Thus microhabitat differentiation is greatest amongst the species which are most dependent on the substratum for food and reproduction: the territorial herbivores. They feed on benthic algae and lay their eggs on the substratum where they are guarded until they hatch (Thresher, 1984). Most planktivores depend on the substratum only for shelter, being broadcast spawners (Thresher, 1984) and feeding entirely on water-borne food. Omnivores typically lie somewhere between these extremes, deriving a substantial proportion of their food from the substratum and in some cases being demersal spawners whilst in others being broadcast spawners (Thresher, 1984).

For most species, zonation patterns at Jeddah were qualitatively virtually identical between years despite large changes in the abundance of some species indicating that the patterns observed do not simply arise through chance factors but have a deterministic basis. Similarly, zonation patterns of species between sites are very alike although again, levels of abundance vary widely (up to an order of magnitude or more). Zonation patterns of some species do differ though. The planktivorous damselfish C. dimidiata and C. ternatensis at the northerly Al Wadj and Tiran sites reach peak abundance at 6m rather than 1.5m as at the other sites. However, such changes can often be explained by differences in conditions between sites. For example, at the Tiran and Al Wadj sites the tidal range was greater than at the more southerly sites, exposing the reef-edge (1.5m) zone at each low tide, and this probably accounts for the deeper distributions of these planktivores.

Such consistency in zonation patterns both within-sites and between-sites could arise in three ways: (1) differential mortality of juveniles after random recruitment over the whole reef, (2) post-settlement movement of newly recruited fish, or (3) habitat selection by larval fish at settlement. In the following we examine the role played by each of these processes in creating the observed zonation patterns of damselfish on Red Sea Reefs.

If differential mortality of juveniles is the mechanism by which these patterns arise, then the bulk of this mortality must occur very

rapidly after settlement since immediate post-settlement juveniles of most species are rarely observed outside the ranges of adult conspecifics, even during periods of peak recruitment (although in some species, such as A. saxatilis and A. sexfasciatus, juveniles are predictably found in reef zones not occupied by adults, Figure 2). Predation pressure on reefs is high with a high ratio of piscivorous predators to prey. Goldman and Talbot (1976) calculate that up to 50% of the fish biomass in some coral reef systems is made up of piscivores. There are few data on the impact of piscivorous fishes on prey populations in reef environments. Sweatman's (1984) study on lizardfish indicates that piscivores on coral reefs are potentially able to eat large proportions of prey populations. In a recent study, Doherty and Sale (1986) found that mortality (presumed due to predation) of recruits was strongly age-dependent and decreased rapidly after metamorphosis (immediately post-settlement). They note that over 25% of individually recognisable fishes disappeared within five days of settlement. Given these high rates of predation, it is possible that zonation patterns could arise through differential mortality in less suitable areas of habitat. Recruits in some parts of the reef may be more susceptible to predation through being weakened by lack of suitable food (but see Shulman, 1984), non-availability of shelter sites (e.g. Shulman, 1985a), or harassment by other fishes (e.g. Sale et al., 1980; Sweatman, 1985b; Shulman, 1985b). Areas constituting suitable habitat differ between species.

However, Doherty and Sale's (1986) data does not exclude the possibility that fish which disappeared moved after settlement. Indeed, they mention that individuals of sedentary, solitary living species disappeared only half as fast as more mobile or gregarious species. This is consistent with individuals having moved to different areas during the first few days after settlement. Site fidelity in newly settled recruits is very hard to measure in areas of continuous reef since this would require the marking of very small fish, something probably impossible without increasing the mortality of such fish, either directly as a result of marking, or indirectly through increasing their vulnerability to predators. Shulman (1985a), in an experiment looking at predation on juvenile fish living on artificial reefs, states that, if they survive, juveniles settling on such reefs invariably eventually migrate to nearby natural reefs (although this was inferred from the distribution of different size classes of fish among reefs).

One of the assumptions of Sale's (1978) lottery hypothesis is that fishes settle from the plankton into areas of 'free' space on reefs, and that once settled these fishes stay put. A recruit which moves after settlement is supposed to be more at risk from predators by moving further from cover and in unfamiliar surroundings. Shulman (1985a) suggests that juvenile coral reef fish which settle into seagrass habitats, move to reef habitats once they have grown large

enough that the seagrass/algae habitat fails to provide refuge from predators. This is usually within a few days to weeks. Territorial damselfish settling into areas of high adult density often are able to escape adult aggression by darting into holes (Sale et al., 1980). However, they soon outgrow these and become more accessible to adults. At this stage they may be forced to move to a new site (Roberts, 1985; Bartels, 1984). Movement of recruits after random settlement into areas of more suitable habitat thus cannot be excluded as a possible mechanism by which zonation patterns are maintained.

However, habitat selection by recruits at settlement would appear to be an adaptively superior strategy. There is now considerable evidence that many species of coral reef fish have well-developed powers of habitat selection at the time of settlement. Several studies have shown non-random settlement patterns in recruiting fish, certain species settling preferentially into particular microhabitats (Williams, 1980; Sweatman, 1983;1984; Sale et al., 1984; Eckert, 1985; Victor, 1986). Although quantitative evidence is lacking, non-random settlement can be inferred for many other species. For example, some species of territorial damselfish such as Stegastes nigricans live in dense mono-specific colonies. Juveniles are almost never found outside established colonies (CR, personal observations). Shulman (1985a) reports habitat selection in territorial damselfish from the Caribbean, noting that they would not recruit to artificial reefs in seagrass beds but only to areas of natural hard substrate. However, habitat selection is often much more subtle than this. For example, Sweatman (1985a;b) in an experimental study, found that recruits of three species of damselfish preferentially settled into sites with resident conspecifics over sites with resident congeners or vacant control sites.

Very narrow habitat requirements are known for many fish, particularly obvious being the relationship between anemonefishes and anemones (Allen, 1972) and the preference by some species of Dascyllus for a few species of branched corals (Sale, 1971). However, cues by which other species select sites can be less obvious. Thresher (1983) found that reef depth and current strength were important determinants of the abundance of planktivorous fishes on patch reefs (these cues can also account for the observed distribution of planktivorous species on Red Sea reefs). The within-zone differentiation in microhabitat use between a number of species found in the present study supports this. Differences between species in the proportions of different substrata within their home-ranges were often small but consistent.

Patterns of habitat selection may not be the sole agent of microhabitat differences between species. Roberts (1985) has suggested that in the 1m terrace zone of Red Sea reefs, differences in distribution of P1. leucozonus and C. unimaculata arise partially through aggressive dominance of the former over the latter species in

areas occupied by the surgeonfish Acanthurus sohal. Robertson and Polunin (1981) and Belk (1975) have demonstrated similar cases of distributional differences between damselfish species being mediated by aggressive dominance.

In contrast, Sale et al. (1984) argue that habitat preferences play only a small part in determining the structure of fish communities on coral reefs. They consider that pre-settlement factors acting on the survivorship and distribution of fish larvae have a greater effect and go further in explaining the temporal instability of patch reef fish assemblages which they and others have found (Williams, 1980; Doherty, 1983; Victor, 1983; Sale et al., 1984; Sale and Douglas, 1984; Eckert, 1984; Shulman, 1985c). At the scale of small patch reefs this is almost certainly so. However, the relative predictability of abundance distributions over reefs which was found in this study, despite sometimes large differences in absolute abundance of species both within- and between-sites, suggests that habitat effects are more important than this. The sampling of large areas of reef in this study eliminates much of the small-scale variability inherent in studies of small patch reefs, allowing underlying pattern to become apparent. Whilst the majority of habitat selection probably takes place at the time of settlement, as argued previously, continuous reefs provide more opportunity for post-settlement movement of fishes to more favourable habitats than do patch reefs. Small fish are very vulnerable to predation in the open spaces between patch reefs (Shulman, 1985a), more so than when moving across areas of continuous reef where cover is plentiful.

This is not to say that at small scales, patches of habitat on continuous reef have predictable, equilibrium communities. Sale (1974; 1979) has clearly demonstrated that this is not so for territorial, herbivorous damselfishes. There are undoubtedly high turnover rates for other species at this scale. The scale at which the reef is studied has had a large effect on the conclusions drawn about fish community structure and has contributed in a large part to controversy within this field (Bohnsack, 1983; Ogden, 1986).

This study shows that amongst damselfish, habitat factors have an important influence on species distributions over the reef and that the strength of these influences depends in part on the intimacy of association a species has with the substratum.

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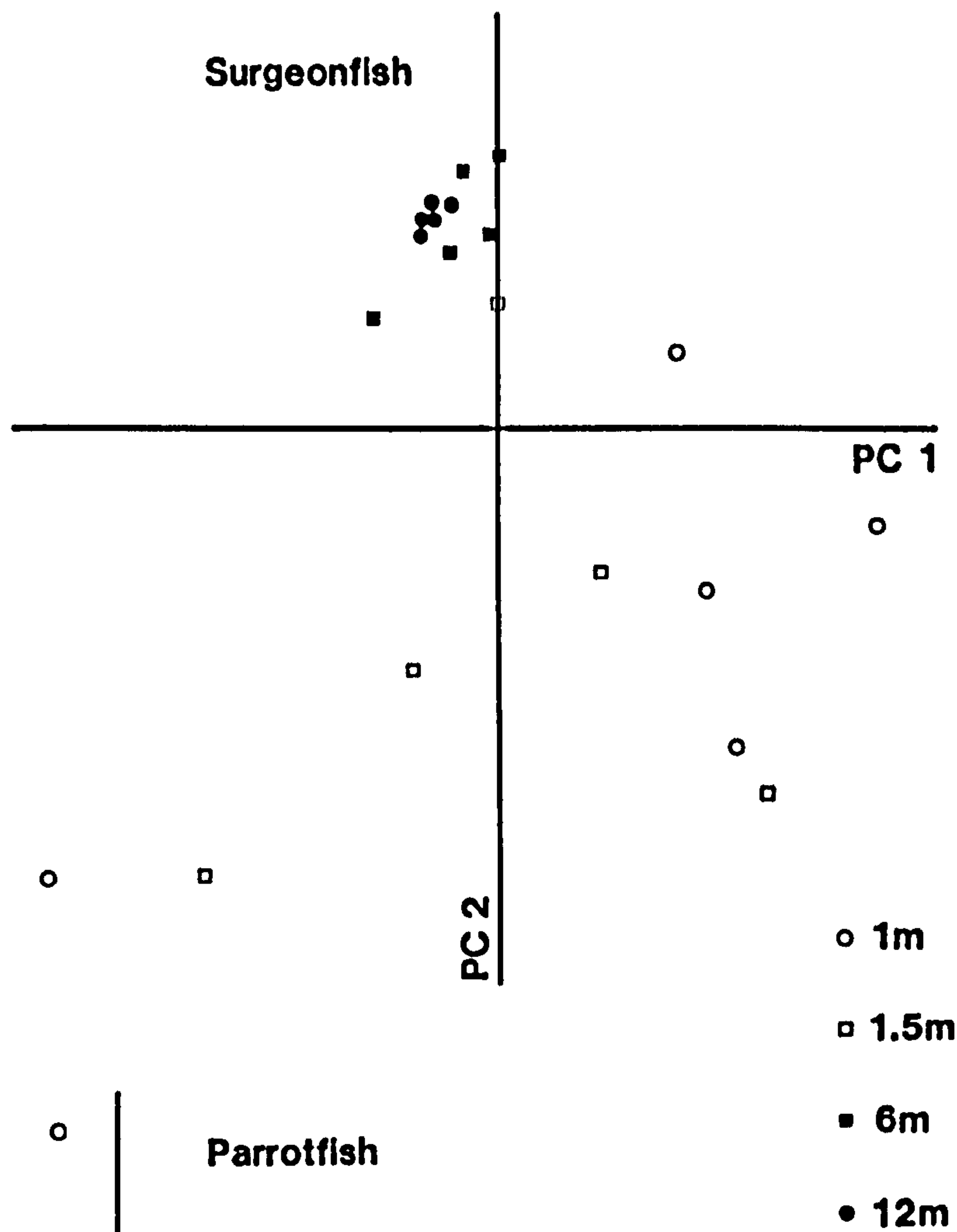
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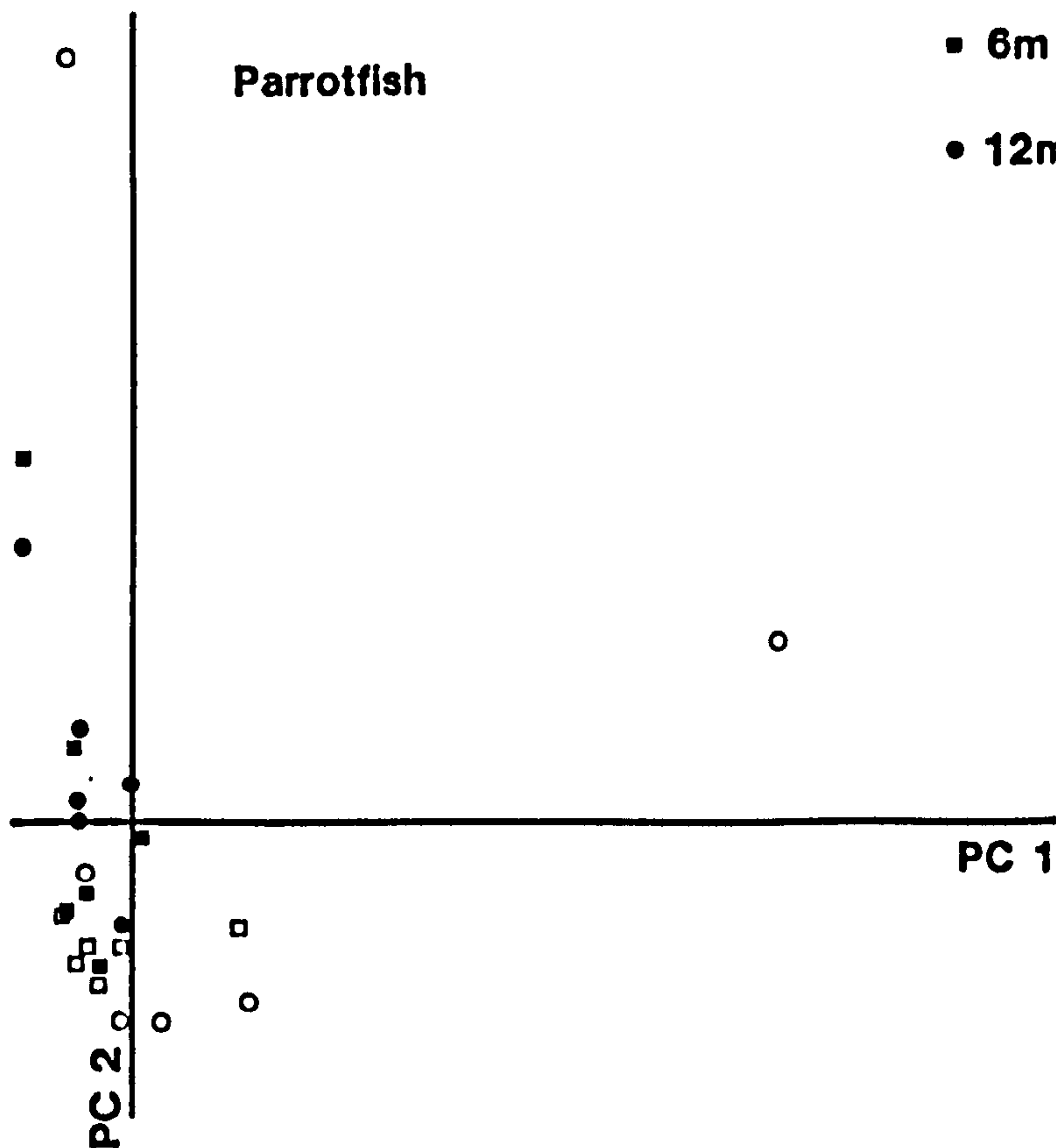
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(a)



(b)



ADDITIONAL NOTE: Principal component plots of transect counts from five sites for surgeonfish (a) and six sites for parrotfish (b). Components 1 & 2 account for (a) 85.9% and (b) 81.1% of the variance in the data.

Surgeonfish and parrotfish were also counted along the 200 x 5m transects laid during the study of damselfish vertical zonation described in the preceding chapter. In order to assess how distinct the four reef zones censused are in terms of their surgeonfish and parrotfish communities, principal components analyses were performed using counts for each family from each transect. For surgeonfish the community inhabiting the reef-face and fore-reef slope zones (6 and 12m) appears relatively distinct and different from that at the reef-edge and on the 1m terrace (1.5m and 1m). The community inhabiting these latter two zones lacks distinctiveness however. Parrotfish communities inhabiting the above zones show high levels of between-site variance and no assemblages characteristic of each zone are apparent.

Chapter 4

**Coral reef fish diversity and abundance and
habitat complexity on Red Sea fringing reefs.**

ABSTRACT

This study looks at the influence of several substrate variables, particularly structural complexity and live coral cover, on coral reef fish species richness and abundance. There have been a number of other similar studies but the results of these have lacked consistency. Most of these have restricted attention only to species very closely associated with the substratum. By looking at fish species with varying strengths of association with the substratum and at different sampling scales, this study aims to assess the scale-dependence of correlations between substrate characteristics and fish community parameters. Fish from five families (Acanthuridae, Chaetodontidae, Labridae, Pomacentridae and Scaridae) were counted by visual census along 200 x 5m transects at four depths at each of four sites. Small fish, closely associated with the substratum, were counted along 10 x 2m transects at five depths at three of these sites. Substrate characteristics were measured from stereophotographs taken at 1m intervals along the 10 x 2m transects at all four sites. Three measures of structural complexity were used: an index of surface area, the variety of different substrata (biological diversity), and numbers of holes of different sizes. Although the depth of peak species richness varied between families, overall there was a trend of increasing species richness with increasing depth. Surface index was a poor predictor of overall species richness but was significantly correlated with pomacentrid species richness and abundance on 200m transects. In contrast, biological diversity of the substratum was highly correlated with overall species richness. Numbers of holes of three sizes taken together accounted for 77% of the variance in overall fish abundance on the 200m transects. None of the measures of structural complexity were significantly correlated with species richness or abundance of small, strongly site-attached fish (10 x 2m transects). Live coral cover was not significantly correlated with species richness or abundance of fish from any family, and only weakly when attention was restricted to obligate corallivorous chaetodontids. This and other studies have ignored the effects of intra- and interspecific interactions on fish distributions and the effects which fish have on the substratum. It is probably this which accounts for the lack of consistency in the results of such studies.

INTRODUCTION

Coral reefs support very diverse fish communities, ranging from around 500-700 species altogether on the reefs in the Caribbean and central Pacific, to 3,000+ on reefs around the Philippines and Indonesia (Goldman and Talbot, 1976; Sale, 1980). The extent to which components of within-habitat and between-habitat diversity contribute to differences in the richness of fish communities between different areas is unclear. Some studies suggest that comparable habitats support more species in areas with larger species pools than with small species pools (Smith, 1978; Walsh, 1985), whilst others suggest that within-habitat diversity is similar between areas with very different sized species pools (Sale, 1980; Talbot and Gilbert, 1981). This study looks at the factors which affect within-habitat diversity in fish communities from the central Red Sea.

Several studies have looked at the relationships between various substrate variables and the species richness and abundance of resident fish communities on coral reefs (Risk, 1972; Luckhurst and Luckhurst, 1978; Gladfelter and Gladfelter, 1978; Carpenter et al., 1981; McManus et al., 1981; Bell and Galzin, 1984; Sano et al., 1984). Several of these studies have found positive correlations between substratum structural complexity and fish species richness or diversity (Risk, 1972; Luckhurst and Luckhurst, 1978; Carpenter et al., 1981). These have restricted attention to small, site-attached species with rather limited ranges of movement.

Correlations between structural complexity and fish abundance have been less consistent. Carpenter et al. (1981) found a strong positive correlation of fish biomass but not abundance with substratum complexity, whilst Luckhurst and Luckhurst (1978) found that fish abundance and substratum complexity were strongly correlated at only one of two sites studied. In Risk's (1972) study, fish abundance and substratum complexity were not significantly correlated (Kendall's tau = -0.10, computed from data in appendices A and B of Risk, 1972). Gladfelter and Gladfelter (1978) suggested that qualitatively, fish abundance on patch reefs increased with increasing structural complexity. However, no quantitative data were obtained to support this claim.

There has also been little consistency between studies concerning the influence of live coral cover. Some studies have found positive correlations between the amount of live coral cover and fish diversity and abundance (Carpenter et al., 1981; Reese, 1981; Bell and Galzin, 1984; Bouchon-Navaro et al., 1985) whilst others have found little or no correlation (Luckhurst and Luckhurst, 1978; McManus et al., 1981; Bell et al., 1985).

In this study we assess the influence of several substrate variables, particularly habitat structural complexity and live coral cover, on species richness and abundance of fish from several

families. We also compare the influence of these variables at two different scales of sampling in order to assess whether the correlations between fish diversity and substratum structural complexity found previously are restricted to strongly site-attached species or whether they are found also with more mobile species.

METHODS

Fish counts

Species of fish from five families were counted along four 200m long, 5m wide transects laid along the fore-reef at four sites on the Saudi Arabian Red Sea coast (Figure 1). Damselfish (Pomacentridae), wrasse (Labridae), butterflyfish (Chaetodontidae) and parrotfish (Scaridae) were counted at all four sites and surgeonfish (Acanthuridae) at three. The transects were laid parallel to the reef crest at depths of 1m (1m terrace), 1.5m (reef-edge), 6m (reef-face) and 12m (fore-reef slope)(Figure 2). Transect width was estimated visually. Species from different families were counted on separate swims along each transect.

Additionally, in order to count fishes very closely associated with the substratum, which could not be accurately or easily counted over 200m transects, five 10m long, 2m wide transects were laid parallel to the reef-crest on the fore-reef at each of three sites: Jeddah south, Jeddah north and Ras Hatiba. These transects were situated at the beginning of the 200m fish transects and were at depths of 1m (1m terrace), 1.5m and 3m (reef-edge), 6m (reef-face) and 10m (fore-reef slope)(Figure 2). Transects were marked using a 10m tape measure. Small, 'resident' species were counted within a 1m band either side of the tape (a total of 20m²) by dividing the transect into ten, 2 x 1m sections (visually estimated). Each section was observed for one minute and individuals of all species were recorded which spent more than thirty seconds of the minute within the section. Individuals whose movements overlapped more than one section were recorded only once. Counts from all ten 2m² sections from each transect were pooled prior to analysis.

Measurements on the substratum

Stereophotographs were taken at 1m intervals along each of the 10m transects used for counting resident fish. Although fish were not counted along 10m transects at Rabigh, five transects were also laid at this site as above, and stereophotographs taken. Five photographs were chosen randomly from each transect and structural complexity measured from a 1m² area within each photograph. Structural complexity was estimated using Dahl's (1973) method. Dahl's surface index (S.I.) is the ratio of the actual surface area to that of a plane with the same dimensions (in this case 1m²). The actual surface area within quadrats is measured by approximation. The scale of measurement is important since the smaller the units used, the greater will be the perceived surface area (Bradbury and Reichelt, 1983). The scale used in this study was one appropriate to fish, the finest resolution being of 1cm. This was also approximately the finest level of detail which

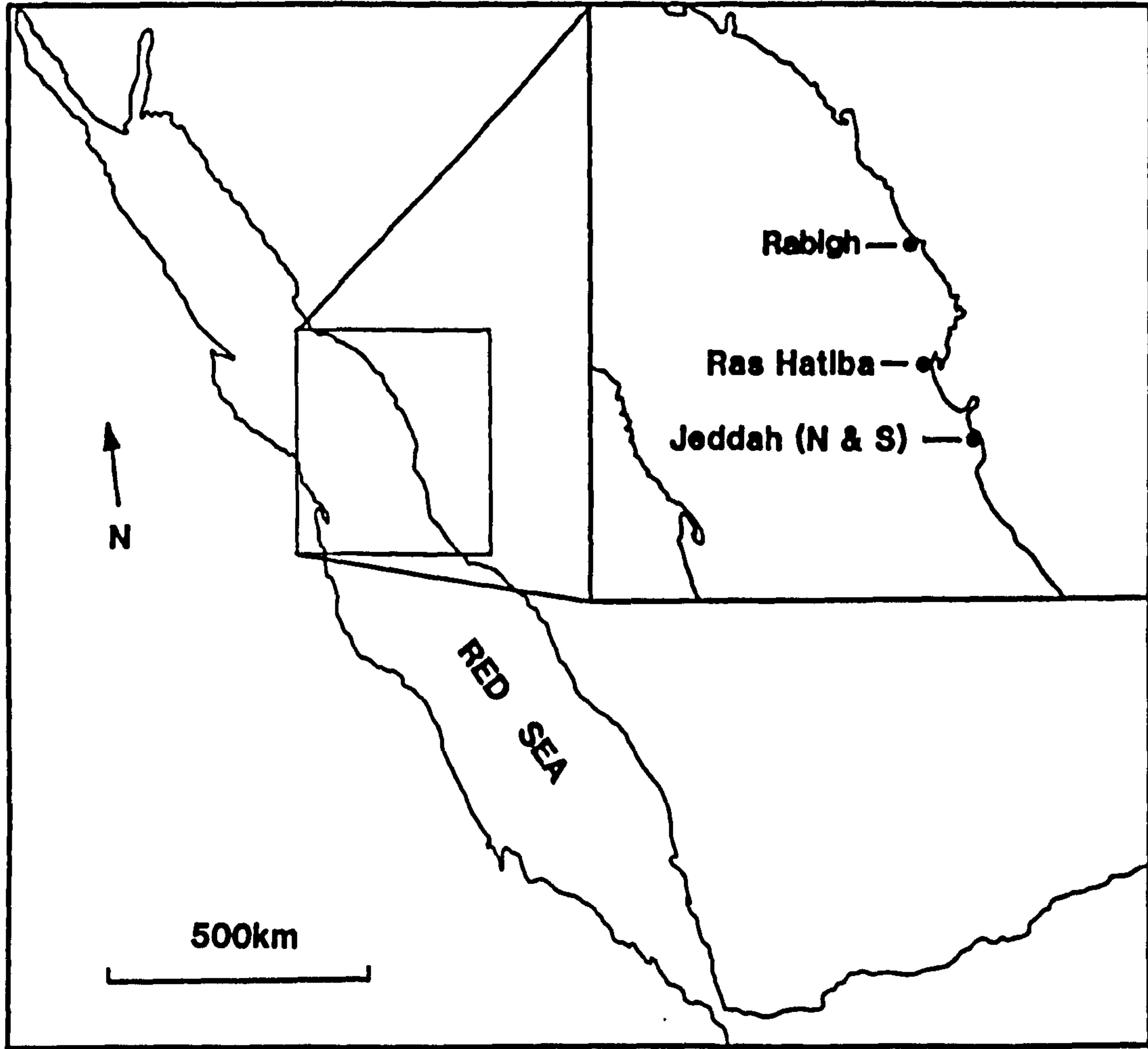


Figure 1: Locations of the four study sites on the Saudi Arabian Red Sea coast.

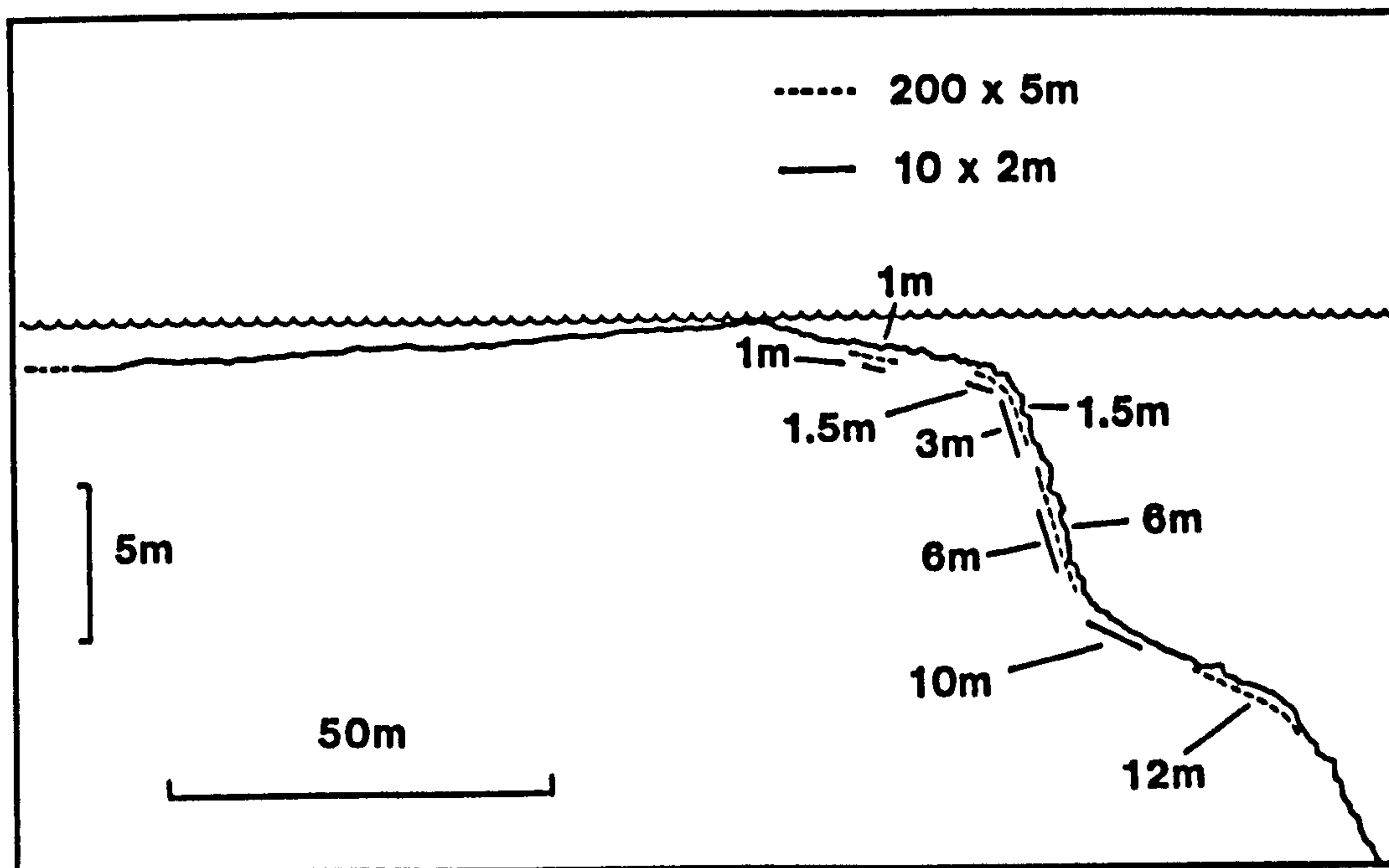


Figure 2: Typical profile of the fringing reef at the four study sites showing the locations of the 200 x 5m fish count, and 10 x 2m fish count and stereo-photographic, transects.

could be resolved accurately from the stereophotographs. With Dahl's method, features of the reef are approximated as geometric shapes, each of which has a particular surface index. For example, a hemisphere has a surface index of 2. The surface indices of the eighteen most common substrata found within the transects were estimated prior to analysis of the photographs. Any other substrata present within the quadrats had their surface indices calculated when they were encountered. The percentage cover of each substratum within the quadrats was estimated visually from the stereophotographs using the transect line (tape measure) for scale. This has proven to be a relatively accurate method for measuring the composition of the substratum (Done, 1981). The percent cover of each substratum (expressed as a proportion) was then multiplied by its surface index and these summed to give an overall surface index for each quadrat. Hence, a flat quadrat, with a 25% cover of hemispherical corals has a surface index of:

$$\text{S.I.} = (0.25 \times 2) + (0.75 \times 1) = 1.25$$

For the purposes of comparison of fish community (200 x 5m transects) and substratum characteristics, results from the 1.5m and 3m depth phototransects were averaged since both of these fall within the bounds of the 1.5m fish transect (Figure 2). Similarly, the 10m phototransect and the 12m fish transect were comparable. Phototransects and fish transects at 1m and 6m were directly comparable.

The percentage cover of different substrata on the 10m transects were also measured using the method of Loya (1978). The number of centimetres of the tape measure covering each substrate type, expressed as a percentage of the total transect length, gives an unbiased estimate of their cover. Hard and soft corals were classified into recognisable taxonomic units for this analysis.

As a second measure of the complexity of the substratum along the transects, the Shannon-Wiener index, H' , was calculated from the percentage cover data of different substrate types from each depth to give a measure of 'biological diversity' (Risk, 1972).

Holes are very important to small fish on coral reefs as refuges from predators. The numbers of holes were also counted within the same five lm^2 quadrats on each transect from which surface indices were calculated. They were classified into the following size ranges (entrance diameter): 0-5cm, 6-15cm, 16-30cm, 31-50cm and >50cm.

RESULTS

Patterns of species richness and abundance

Figure 3 shows patterns of species richness over the reef at the four study sites for species from each family. There is considerable between-site variation in patterns of species richness for all families. The depth at which species richness is greatest varies between families. Overall though, for the five families pooled, there is a general trend of increase in species richness with increasing depth.

Figure 4 shows patterns of abundance for each family. For three families, butterflyfish (Chaetodontidae), wrasse (Labridae) and damselfish (Pomacentridae), patterns of abundance distribution are relatively consistent between sites. In contrast, patterns of abundance for parrotfish (Scaridae) and surgeonfish (Acanthuridae) vary widely between sites. The overall abundance distribution is very similar to that for damselfish with peak numbers being found at the reef-edge (1.5m). This pattern is largely due to the influence of abundant planktivorous damselfish but is reinforced by similar patterns in wrasse and butterflyfish.

There is a great deal of between-site variability in both abundance and species richness of fish on the 10 x 2m transects, and no consistency of patterns is apparent (Figure 5).

Structural complexity

Patterns of structural complexity (S.I.) were very similar between all sites although some had a generally higher level of complexity than others (Figure 6a). At all sites surface index was highest between 3m and 6m deep. Biological diversity of the substratum was much more variable between sites (Figure 6b).

The depth distributions of holes of different sizes are shown in Figure 7. This is a more direct measure of the availability of shelter to fish than either surface index or biological diversity. Again, there is considerable variability between sites. However, in general the largest numbers of holes of all sizes are found between 1.5m and 6m deep.

Relationships between substrate variables and the fish community

Kendall's rank correlation coefficients were calculated in order to assess the relationships between substrate variables and counts of fish from the 200 x 5m and 10 x 2m transects. Because a large number of these were calculated, a significance level of $P < 0.01$ was used to reduce the chances of making a Type I error (accepting that two variables are significantly correlated when they are not).

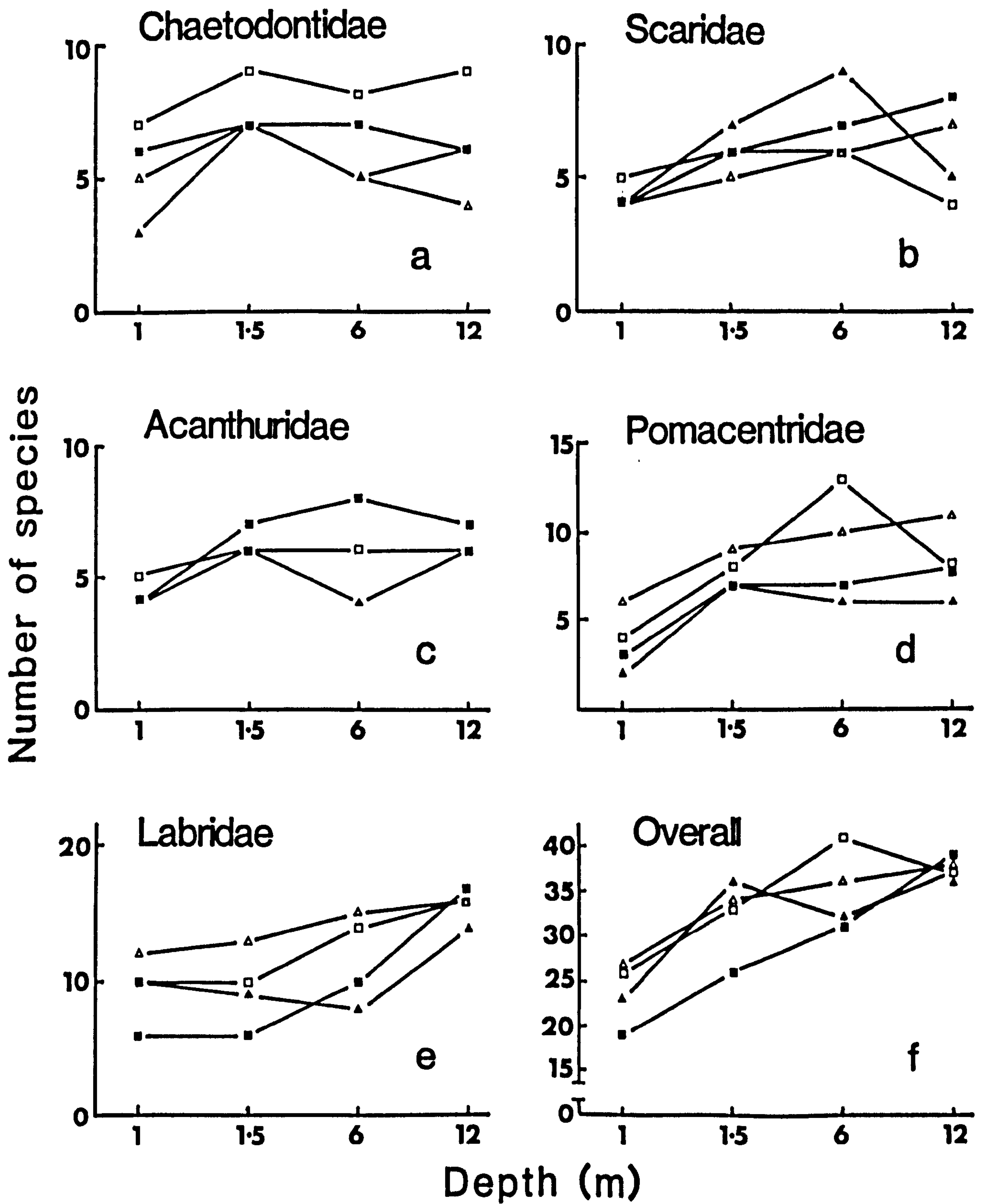


Figure 3: Patterns of species richness of fish from the five families studied. ■ Jeddah south site, □ Jeddah north site, △ Ras Hatiba, and ▲ Rabigh.

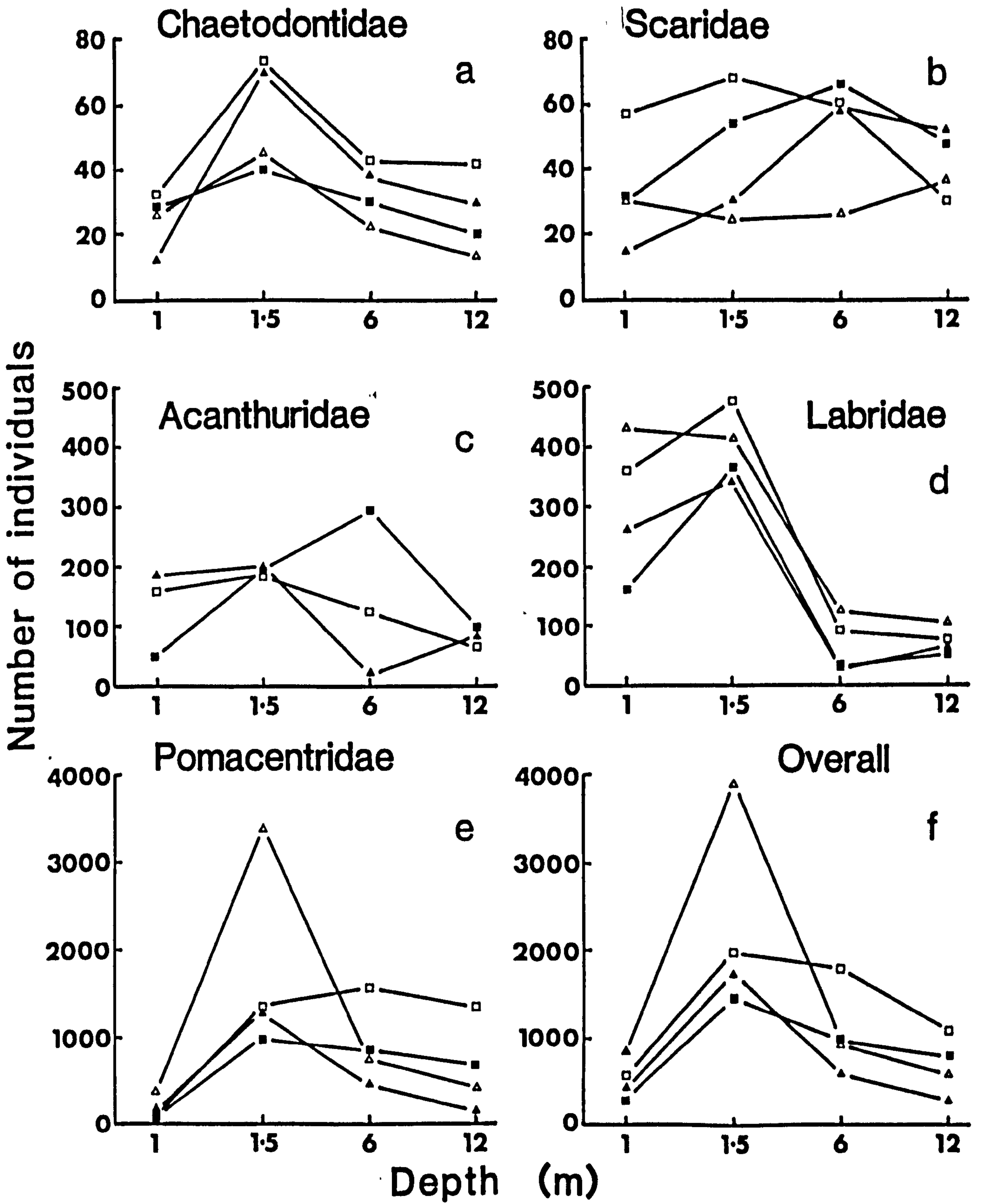


Figure 4: Abundance distributions of fish from the five families studied. ■ Jeddah south site, □ Jeddah north site, △ Ras Hatiba, and ▲ Rabigh.

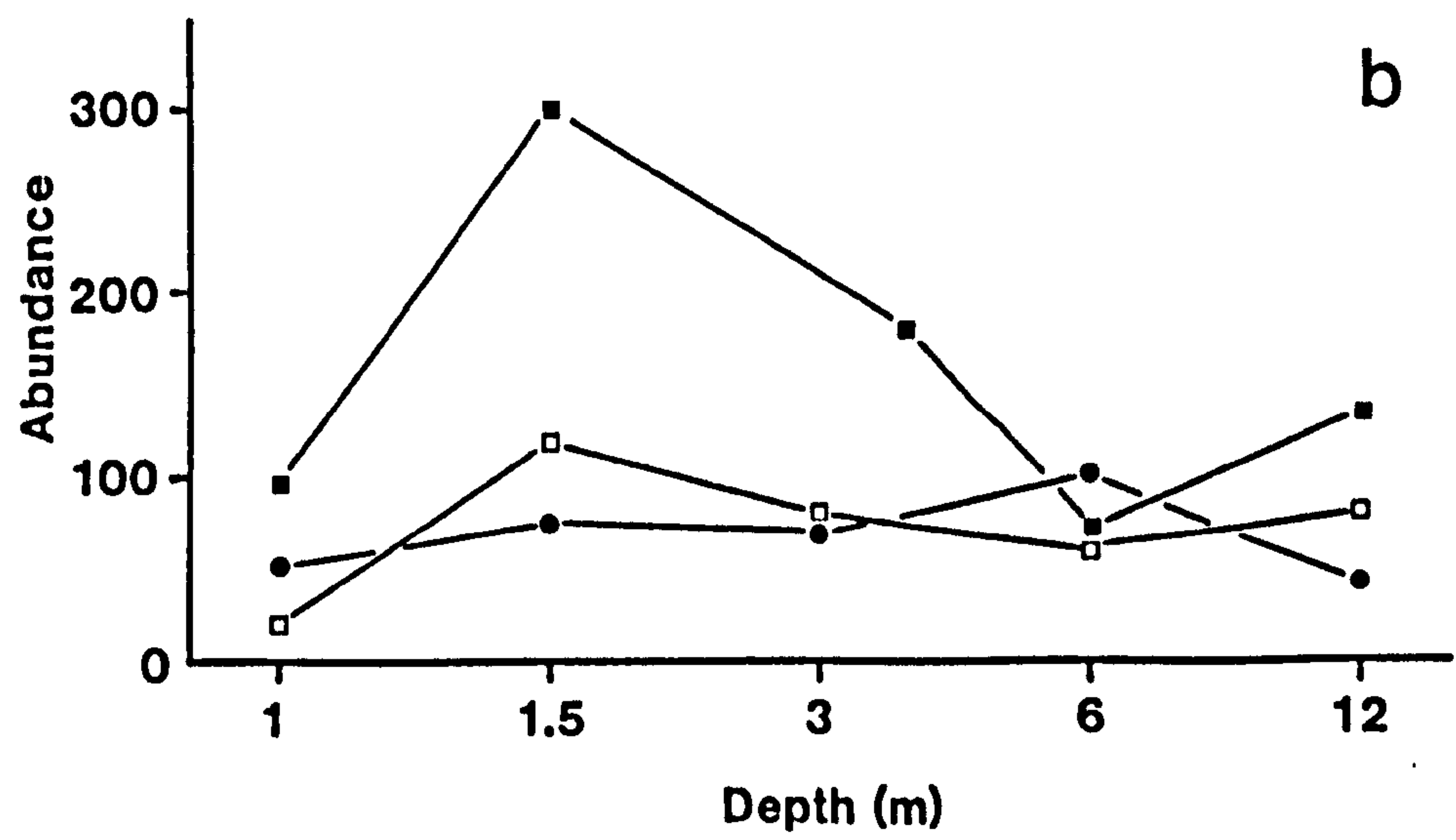
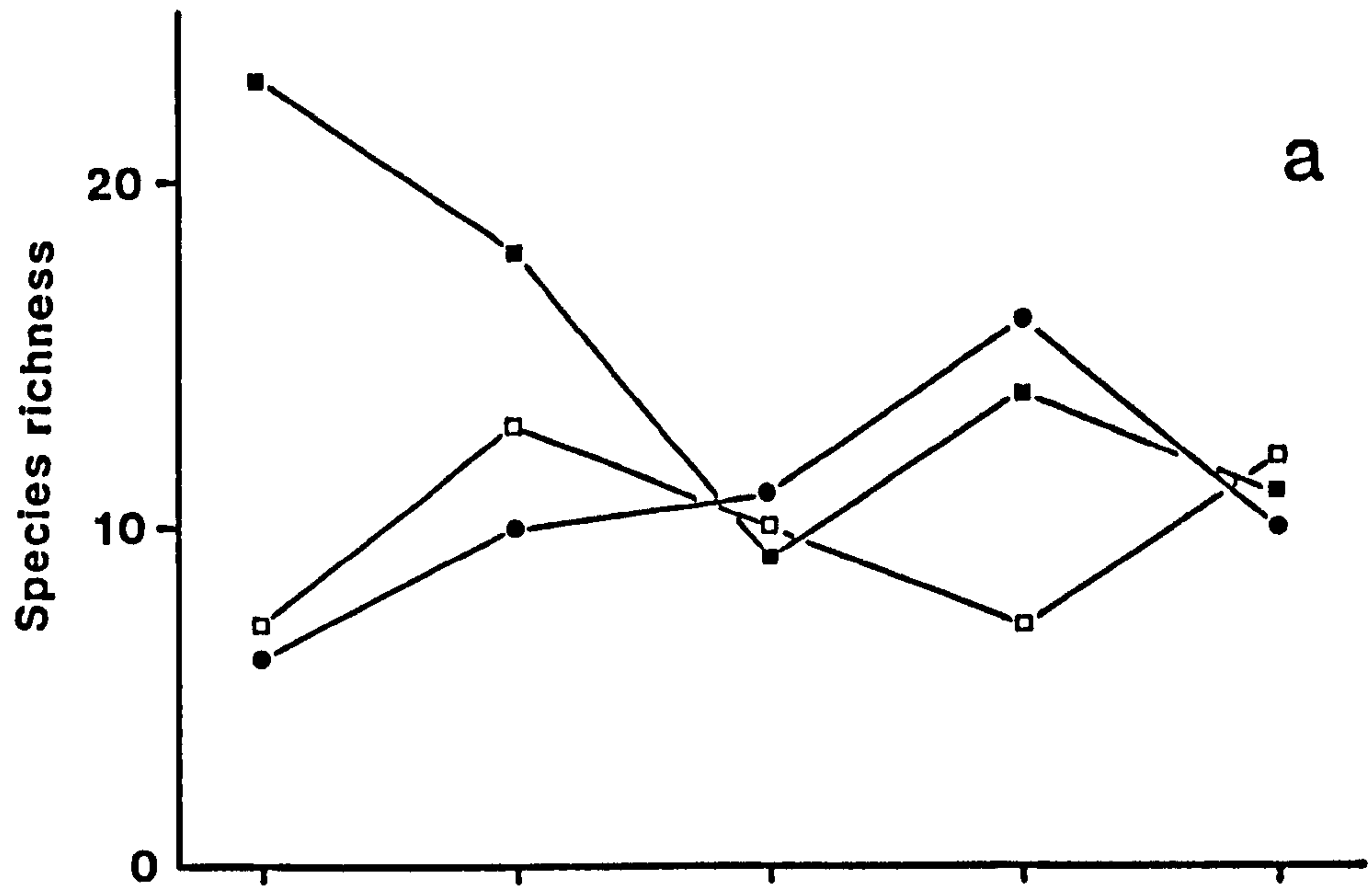


Figure 5: (a) Species richness, and (b) abundance of fishes counted on 10 x 2m transects. □ Jeddah south, ● Jeddah north, and ■ Ras Hatiba.

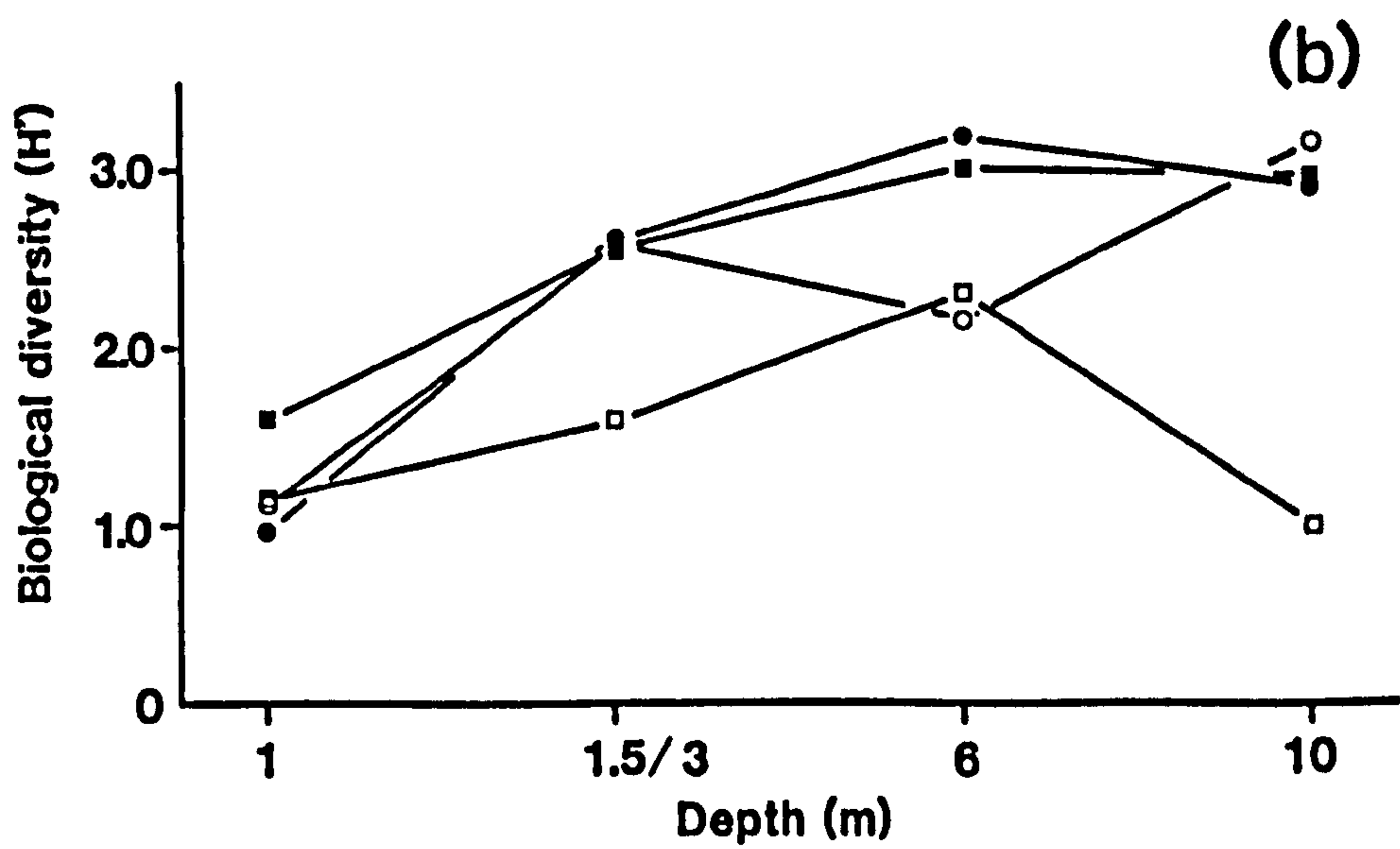
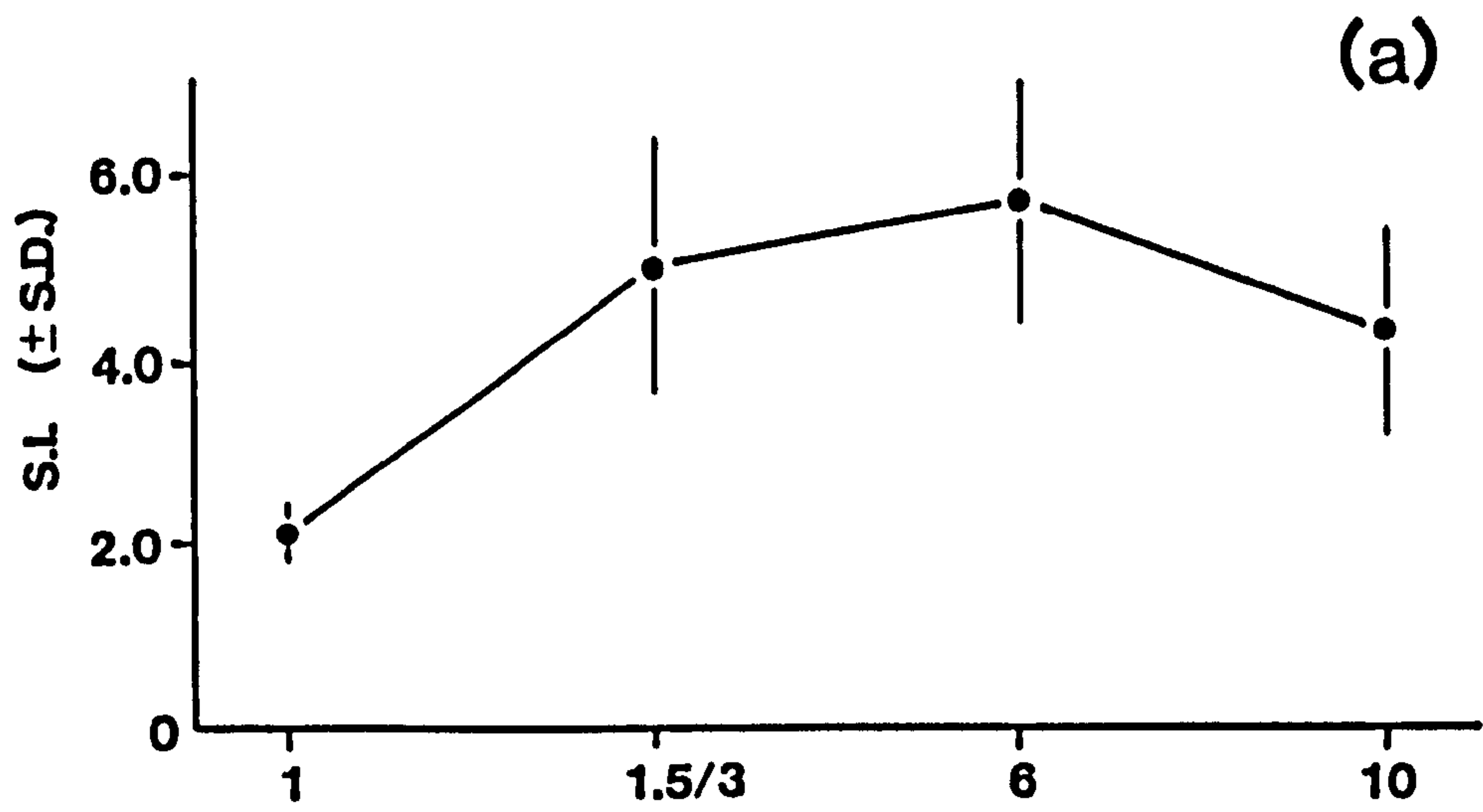


Figure 6: (a) Pattern of average structural complexity (surface index), and (b) of biological diversity of the substratum over the reef from the four study sites. Symbols in (b) □ Jeddah south site, ● Jeddah north site, ■ Ras Hatiba, and ○ Rabigh. In both cases the figures given for 1.5m depth are derived from pooled values from transects at depths of 1.5 and 3m.

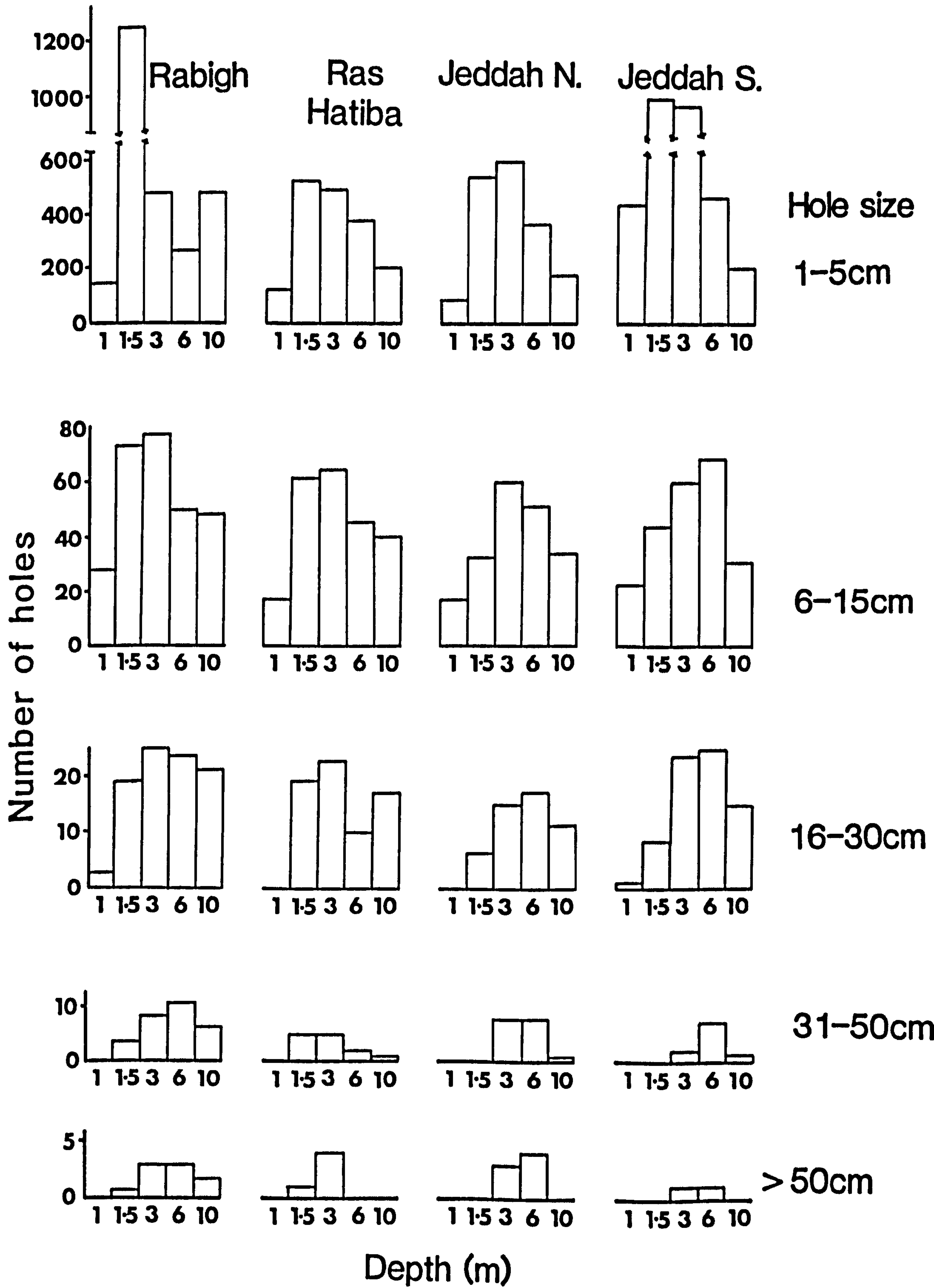


Figure 7: Depth distribution of holes of different sizes at the four sites studied.

Structural complexity Structural complexity of the substratum (as measured by surface index) is significantly correlated only with damselfish abundance (tau = 0.52) and damselfish species richness (tau = 0.48). However, both of these correlations are weak. S.I. does not correlate significantly with either abundance or species richness of fishes on the 10 x 2m transects.

Biological diversity In contrast to Risk's (1972) findings that biological diversity of the substratum was a poor predictor of species diversity, in this study overall fish species richness (on 200 x 5m transects) was highly positively correlated with this measure (tau = 0.81) as Figure 8 shows. Note that the data include one outlier, the deep transect from a site damaged by human activity, and that for this reason this point was excluded from the calculation of correlation and the fitted regression line. However, biological diversity was not significantly correlated with overall fish abundance (200 x 5m transects) nor with abundance or species richness of fish on the 10 x 2m transects.

Depth Depth alone is also a relatively good predictor of overall species richness (tau = 0.68) and so a stepwise multiple regression was performed to look at the relative effects of depth, biological diversity and surface index. The addition of neither depth nor surface index significantly increased the proportion of the variance in species richness explained by biological diversity alone ($r^2 = 0.90$).

Numbers of holes The availability of shelter, as measured by numbers of holes, was not correlated with overall species richness or abundance on either 200 x 5m or 10 x 2m transects. However, numbers of holes of 16-30cm and 31-50cm were correlated with parrotfish species richness (tau = 0.51 and 0.50 respectively), but not abundance, and holes of 6-15cm and > 50cm were correlated with damselfish abundance (tau = 0.56 and 0.54 respectively), but not with species richness. Numbers of holes > 50cm diameter were also correlated with butterflyfish abundance (tau = 0.56).

Since none of the substrate variables measured in this study individually accounted for much of the variance in overall fish abundance (on 200 x 5m transects), a stepwise multiple regression of all substrate variables on total fish abundance was performed. The results are shown in Table 1. Individually, the numbers of holes > 50cm diameter explain the largest amount of the variance in abundance, but addition of numbers of holes of 31-50cm and 6-15cm significantly improve the correlation. Overall, these three variables account for 77% of the variance in total fish abundance.

Live coral cover The percentage cover of live scleractinian corals

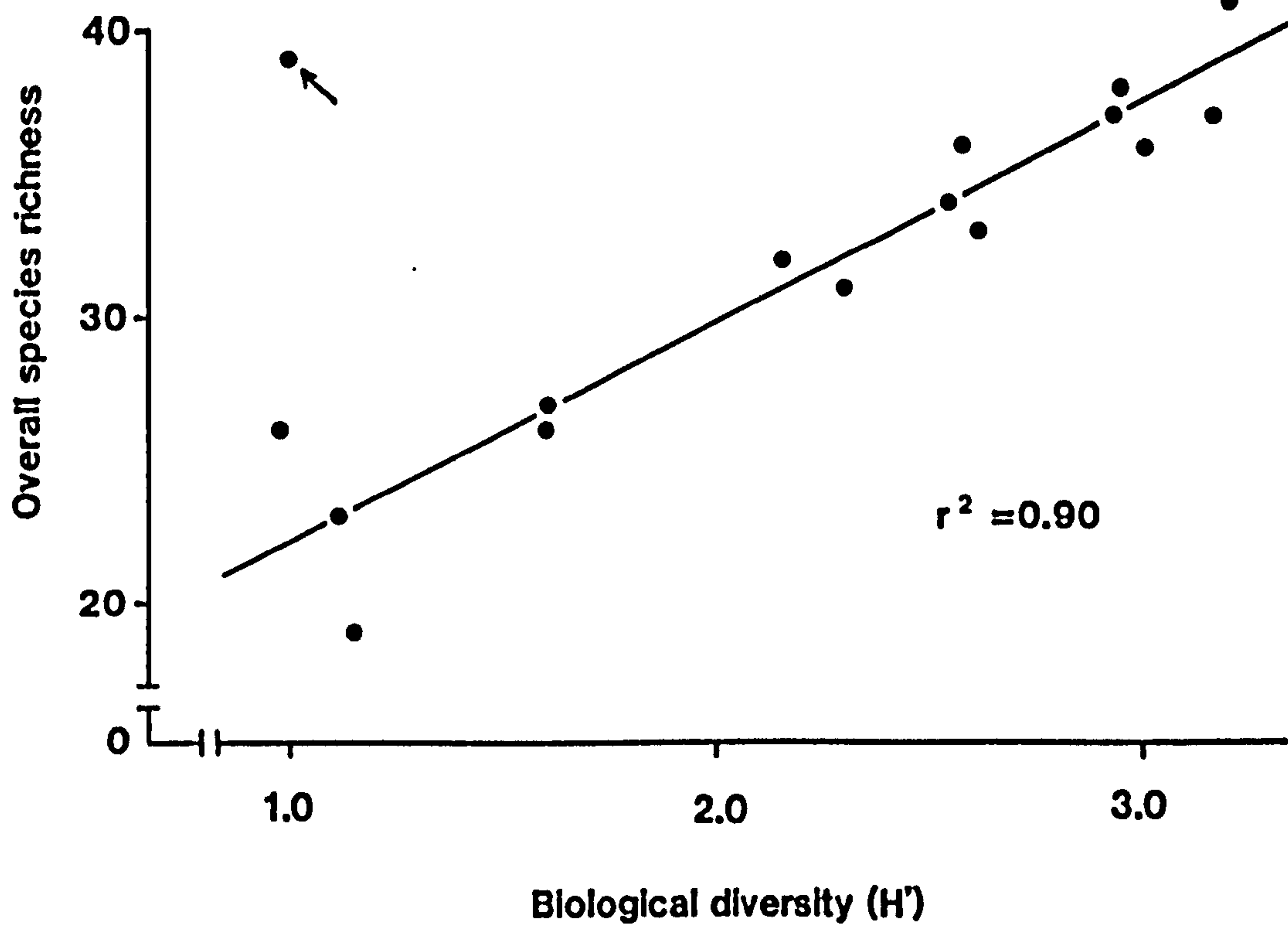


Figure 8: Relationship between biological diversity of the substratum and fish species richness. The outlying point (arrowed) was excluded from the calculation of the fitted regression line for reasons given in the text.

VARIABLE	% VARIANCE EXPLAINED
No. of holes > 50cm - alone	32.2*
No. of holes 31-50cm - additional	19.2*
No. of holes 6-15cm - additional	25.4**
Total	76.8%

Table 1: Stepwise multiple regression analysis of substrate variables on overall fish abundance.

* = $P < 0.05$; ** = $P < 0.01$.

did not correlate significantly with abundance or species richness of any of the fish families in this study, nor with overall abundance or species richness on the 200 x 5m or 10 x 2m transects. Several studies have suggested that butterflyfish abundance is related to the abundance of live corals (Bouchon-Navaro et al., 1985; Reese, 1977; 1981). However, not all butterflyfish are corallivores and so a separate analysis was performed looking only at the abundance of the three species of obligate coral feeding butterflyfish in the Red Sea: Chaetodon austriacus, C. larvatus, and C. trifascialis (Harmelin-Vivien and Bouchon-Navaro, 1981). Individually, the abundance of none of these species correlates significantly with live coral cover. However, the pooled abundance of the three species correlates significantly, but only weakly, with coral cover ($\tau = 0.39$, $P < 0.05$).

Other substrate variables Of the other substrate variables measured (soft coral cover, filamentous algal cover and coralline algal cover) soft coral cover was significantly positively correlated with wrasse species richness ($\tau = 0.50$), damselfish species richness ($\tau = 0.57$) and overall species richness ($\tau = 0.59$). However, the effect of this variable is confounded with depth ($\tau = 0.59$) and biological diversity ($\tau = 0.74$). Filamentous algal cover and coralline algal cover were not significantly correlated with abundance or species richness of any family or with overall abundance or richness of fish on 200 x 5m or 10 x 2m transects.

DISCUSSION

Three previous studies, concentrating on small, strongly site-attached species, have found strong quantitative relationships between species richness or diversity of fishes and measures of structural complexity on coral reefs (Risk, 1972; Luckhurst and Luckhurst, 1978; Carpenter et al., 1981). However, in this study, surface index, a measure of structural complexity comparable to those used in these studies, was found to be only very weakly correlated with overall fish species richness from the 200 x 5m transects ($\tau = 0.39$, $P < 0.05$) and not at all with counts of resident fish from the 10 x 2m transects. Depth alone was a much better predictor of species richness than surface index. However, biological diversity of the substratum was highly positively correlated with overall fish species richness from the 200 x 5m transects. This is exactly the opposite pattern to that found by Risk (1972) in the Virgin Islands where biological diversity was not significantly correlated with fish diversity ($r = -0.16$) but structural complexity was ($r = 0.62$). Direct measurements of the availability of shelter to fish (numbers of holes) were found not to be correlated significantly with fish species richness.

Increases in fish species richness with habitat complexity are only partially due to increases in the overall abundance of fish. In only three of the five families of fish studied was species richness significantly positively correlated with abundance, and Figures 3 and 4 show that patterns of abundance distribution over the reef are quite different from those of species richness, both within families and overall. In this study, no single substrate variable was found to be a good predictor of the overall abundance of fish. However, numbers of holes of three sizes, taken together account for 77% of the variance in fish abundance over the reef, underlining the importance of shelter to reef fish.

The influence of particular substratum characteristics were not the same on fish from different families (and will not be on species within families although this level of detail is not considered in this study). Those species which are small and remain close to the substratum might be expected to be influenced most by local substratum characteristics. Hence, Risk (1972), Luckhurst and Luckhurst (1978) and Carpenter et al. (1981) confined their attention entirely to such species. Most damselfish species are strongly site-attached, having only small territories or home-ranges (Sale, 1974;1978; Fricke, 1975). Within only this family was surface index significantly positively correlated with abundance and species richness. Species within the butterflyfish family range from having small home-ranges and territories to quite extensive ones. However, butterflyfish abundance is not significantly positively correlated with any measure of substratum complexity except numbers of holes > 50 cm diameter ($\tau = 0.56$). Wrasse also have a very wide range of home-range and territory

sizes and none of the measures of complexity correlate significantly with either species richness or abundance of this family. Surgeonfish and parrotfish are generally wide-ranging, occupying quite large areas of reef. However, parrotfish species richness does correlate significantly with the numbers of holes of 16-30cm and 31-50cm diameter whilst overall, surgeonfish are not significantly associated with any substrate variable. These data thus qualitatively seem to support the view that the composition of the substratum has a stronger local influence on resident communities of small, strongly site-attached species. However, data from the 10 x 2m transects, in which only such species were recorded, do not. On these transects neither abundance nor species richness were significantly correlated with any substrate variable. Why it is that such species appear not to be strongly influenced by the substratum at these sites in the Red Sea but are at sites in the Caribbean and Pacific is not known.

The amount of live coral cover was found to have little influence on the abundance or species richness of fish from any family. Even when attention was restricted only to obligate corallivorous butterflyfish species, only a very weak association was found. Bell and Galzin (1984) in a study of a lagoonal fish community on a Pacific atoll, concluded that percentage live coral cover had a strong positive influence on both total species richness and abundance of the resident community. However, this site was somewhat atypical since at the time of the study, much of the coral had recently been killed by periods of prolonged low tide. In a further study at a much larger scale, Bell et al. (1985) found that coral cover and butterflyfish abundance and diversity were only weakly correlated with the amount of live coral but noted that rich and abundant butterflyfish assemblages were only found at sites rich in coral. However, Bouchon-Navaro et al. (1985) were able to demonstrate significant correlations between the density of coral feeding butterflyfish and amount of live coral cover during two studies at a site in Moorea, French Polynesia. Live coral cover was greatly reduced between these two studies by an infestation of the crown-of-thorns starfish, Acanthaster planci. Sano et al. (1984), in a series of experiments using living and dead branching corals, have reported that overall, dead colonies support fewer individuals and species of resident fishes than do live colonies.

Reese (1977, 1981) suggested that the abundance of obligate corallivorous butterflyfish species be used as an indicator of the 'health' of coral reefs, healthy reefs being those with large amounts of live coral cover. He developed the argument that coral feeding species would respond to changes in the coral community before direct measurements on this community would show that a reef had been damaged. However, the evidence that the abundance of coral feeding butterflyfish is strongly influenced by the amount of coral cover is equivocal. In addition, many healthy and undisturbed reefs have naturally low levels of coral cover (e.g. Sheppard, 1985). This study

supports the view of Bell et al. (1985) that abundance of corallivorous butterflyfish species is a poor indicator of live coral cover (and hence reef health) and that high levels of between-site variability in abundance would mask variations due to changes in the coral community within sites.

The distribution of fish on coral reefs is not only influenced by the composition of the substratum. In particular, this study has ignored the effects of interspecific interactions on fish distribution. For example, territorial herbivorous surgeonfish and damselfish can have an important influence on the distribution of other herbivorous species, particularly parrotfish (Robertson et al., 1979; Roberts, 1985; Robertson and Gaines, 1986; but see Choat and Bellwood, 1985). The territorial activities of these species also affect the composition of the substratum, altering patterns of live coral cover (Dart, 1972; Neudecker, 1979; Sammarco and Carleton, 1981) and, as a consequence, habitat structural complexity. Hence it is impossible to assess the effects of different substrate variables on fish abundance and species richness in isolation without experimentation, since the substratum is not independent of the fish community. It is probably largely because of this interdependence that, in this study, most of the substrate variables measured were found to be poor predictors of fish species richness and abundance either within families or at the community level. This is also likely to be the reason for the large discrepancies between the results of similar studies from different regions.

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Chapter 5

Resource sharing in territorial herbivorous reef fishes.

Errata:

- (1) Istiblennius periophthalmus is correctly known as Istiblennius periophthalmus.
- (2) In the Abstract, page 129, Pomacentrus aquilis should Pomacentrus aquilus.
- (3) Salarius fasciatus is correctly known as Salarias fasciatus.

RESOURCE SHARING IN TERRITORIAL HERBIVOROUS REEF FISHES

PARTAGE DES RESSOURCES CHEZ LES POISSONS HERBIVORES TERRITORIAUX DES RECIFS

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ABSTRACT

Two symbiotic associations of territorial, herbivorous reef fishes from the Red Sea are described. The first, from central and northern regions, involves a surgeonfish (Acanthurus sohal), two damselfish (Plectroglyphidodon leucozonus cingulum and Chrysiptera unimaculata) and two blennies (Cirripectes castaneus and Istiblennius periophthalmus). The second, from the south, involves the same surgeonfish, two damselfish (Pomacentrus trilineatus and P. aquilis) and two blennies (Salarius fasciatus and C. castaneus). Territories of these species overlap extensively. Both surgeonfish and damselfish contribute to interspecific defence of territory areas. Damselfish aggress against smaller individuals on average than the surgeonfish and the joint defence leads to almost total exclusion of non-territorial herbivores. There are few aggressive interactions between A. sohal and cohabitant damselfish. Surgeonfish appear to tolerate damselfish as the cost of doing so is low compared to the cost of exclusion because damselfish (1) contribute to the defence of the algal lawn, and (2) have refuge holes into which they retreat when aggressed against and so would be energetically expensive to exclude.

Blennies do not interspecifically defend algal lawn and exist as food parasites of the surgeonfish and damselfish. In the southern association there is intense aggression between P. trilineatus and blennies but this fails to exclude them. However, in the central and northern association, there is little aggression between damselfish and blennies. A. sohal never aggresses against blennies.

In contrast, Plectroglyphidodon lacrymatus are colonial, herbivorous damselfish which do not share territories with A. sohal. Levels of intraspecific aggression are much lower and interspecific aggression higher than in A. sohal associates.

RESUME

On a étudié 2 types d'association symbiotique territoriale chez les poissons herbivores de Mer Rouge. La première, observée dans le centre et dans le Nord de la Mer Rouge, met en cause le poisson chirurgien (Acanthurus sohal), 2 poissons demoiselles (Plectroglyphidodon leucozonus cingulum et Chrysiptera unimaculata) et 2 blennies (Cirripectes castaneus et Istiblennius periophthalmus). La seconde observée dans le sud de la Mer Rouge, inclut le même poisson chirurgien, deux autres demoiselles (Pomacentrus trilineatus et P. aquilis) et deux autres blennies (Salarius fasciatus et Cirripectes castaneus). Dans chaque cas, les territoires de ces espèces se chevauchent en grande partie. Les poissons chirurgiens et, à un niveau moindre les poissons demoiselles contribuent à la défense interspécifique des territoires. En général, les poissons demoiselles sont plus agressifs que les chirurgiens vis à vis des espèces plus petites et la défense conjointe conduit à l'exclusion presque totale des herbivores non-territoriaux. Il existe quelques rares interactions agressives entre A. sohal et ses voisins demoiselles. Il semblerait que les chirurgiens tolèrent les poissons demoiselles sur leur territoire car ces derniers, qui contribuent à la défense, ont des refuges dans lesquels ils peuvent se retirer en cas d'agression. Les blennies apparaissent comme les parasites alimentaires des poissons chirurgiens et demoiselles. Dans l'association du sud de la Mer Rouge, il existe une intense interaction agressive entre P. trilineatus et les blennies. Dans l'autre association, il y a peu d'agressions entre demoiselles et blennies. Les jeunes poissons demoiselles, qui participent très peu à la défense du territoire apparaissent aussi comme des parasites alimentaires. Au contraire, les Plectroglyphidodon lacrymatus (demoiselles herbivores et coloniaux) ne cohabitent pas avec les A. sohal. Leurs territoires sont protégés avec moins d'agressions interspécifiques qu'il n'y en a entre les associés d'A. sohal, et ceci constitue probablement une adaptation pour la défense du territoire en l'absence des poissons chirurgiens.

INTRODUCTION

Territorial herbivorous reef fish, particularly surgeonfish, damselfish and blennies, browse on a filamentous algal lawn which grows within their territories (Robertson *et al.*, 1979; Lobel, 1980; Nursall, 1981). Surgeonfish and damselfish are interspecifically territorial protecting areas against a wide range of species, primarily herbivores (Low, 1971; Robertson *et al.*, 1979). However, there is often mutual toleration between territory holding species, with little aggression between them. The sharing of algal resources and size differences between species of these families have allowed the development of symbiotic territory sharing (see Robertson and Polunin [1981] for surgeonfish and damselfish). This represents one mechanism which may contribute to high within-habitat diversity of fish in the reef environment by allowing species with similar resource requirements to coexist without competitive exclusion. This study investigates the relationships between cohabitant species of the above families from the Red Sea and attempts to identify the means through which coexistence is achieved.

METHODS

The Study Species

Two associations of territorial herbivores from the Saudi Arabian Red Sea have been observed. In central & northern regions reefs are well developed, clear-water and drop-off steeply into deep water (Ormond *et al.*, 1984). In contrast, reefs of the southern Red Sea, from a latitude of about 20°10'N southwards on the Saudi Arabian coast, are shallow, silty and poorly developed (Ormond *et al.*, 1985). The two regions support markedly different fish assemblages (Roberts and Ormond, in preparation). On central & northern reefs the cohabitant species are *Acanthurus sohal* (surgeonfish), *Plectroglyphidodon leucozonus cingulum*, *Chrysiptera unimaculata* (damselfish), *Cirripectes castaneus* and *Istiblennius periophthalmus* (blennies). On southern reefs cohabitant species include the above surgeonfish, *Pomacentrus trilineatus* and *Po. aquilus* (damselfish), *Salarias fasciatus* and *Cirripectes castaneus* (blennies). Figure 1 shows the distributions of these species and the typical structure of fringing reefs in the two regions.

Species were identified according to Allen and Randall (1980) and Randall (1983). Size differences between cohabitants are marked. Adult *A. sohal* are on average around 30cm long whilst

Pl. leucozonus cingulum, *Pl. lacrymatus*, *Po. aquilus* and *Po. trilineatus* adults average 9-11cm. *C. unimaculata* are smaller and large adults reach 8cm long. *I. periophthalmus* and *S. fasciatus* adults were typically 8-12cm long whilst *C. castaneus* were smaller, attaining a maximum length of 8-9cm.

Territory mapping

A 50m² rope quadrat was laid in an area adjacent to the reef-edge on a fringing reef near Jeddah, Saudi Arabia (central Red Sea). On this part of the reef the distributions of the study species overlap (Figure 1B). The quadrat was divided into two areas of 25m² with a second rope to simplify position fixing whilst mapping. A sketch map was then drawn marking obvious structural characteristics throughout the area. Fish were given a day to get used to the ropes before territory plotting began. Surgeonfish and damselfish territories were plotted by watching each individual for fifteen minutes and marking its position on the map every ten seconds. The positions of aggressive interactions were also marked. Territories of each species were plotted on separate maps. This method provides a rapid and reasonably accurate means of delineating territories (Roberts, in press). Due to the abundance of blennies within the area their territories were not plotted. Instead the positions of refuge holes were recorded (only one per individual being marked).

Feeding by non-territorial herbivores

Intrusion rates To assess the efficacy of territorial defence, eight 2m² rope quadrats were laid within the mapped area and left for one day for fish to become accustomed to them. Each was then observed for thirty minutes and the numbers and species of all non-territorial herbivores feeding within them recorded. These observations were repeated the following day.

Herbivore pressure outside territories *A. sohal* are colonial and colony areas are clearly defined by an abrupt change from filamentous algal dominated substratum to coralline algal dominated substratum (Vine, 1974). The grazing pressure of non-territorial herbivores within such an area adjacent to the reef-edge, 20m from the mapped quadrat, was also measured. Due to the high density of these fish within the area, activities could only be followed within a 1m² quadrat. This was visually estimated. It was not possible to count individual bites made by several herbivores simultaneously so instead an individual was recorded if it entered the area and fed. If it then left and reentered to feed after fifteen seconds or more then it was scored again but if reentry was within fifteen seconds then a second recording was not made.

Aggressive behaviour

Individuals of all territory sharing species except *Po. aquilus* and *I. periophthalmus* were observed for fifteen minutes each and acts of aggression recorded noting (1) the species aggressed against, (2) its estimated length (cm), and (3) the intensity of the interaction. Aggressive intensity was scaled 1-3: 1 = display, 2 = display and movement towards intruder, and 3 = chase. Observations of species from the southern Red Sea were made at Raka (lat. 18°26'N long. 41°25'E) and from the central & northern Red Sea at Jeddah (lat. 21°39'N long. 39°05'E) and Shu'aiba (lat. 20°40'N long. 39°25'E). Observations were also made at Jeddah on *Plectroglyphidodon lacrymatus*, a herbivorous damselfish which holds territories on rubble patches

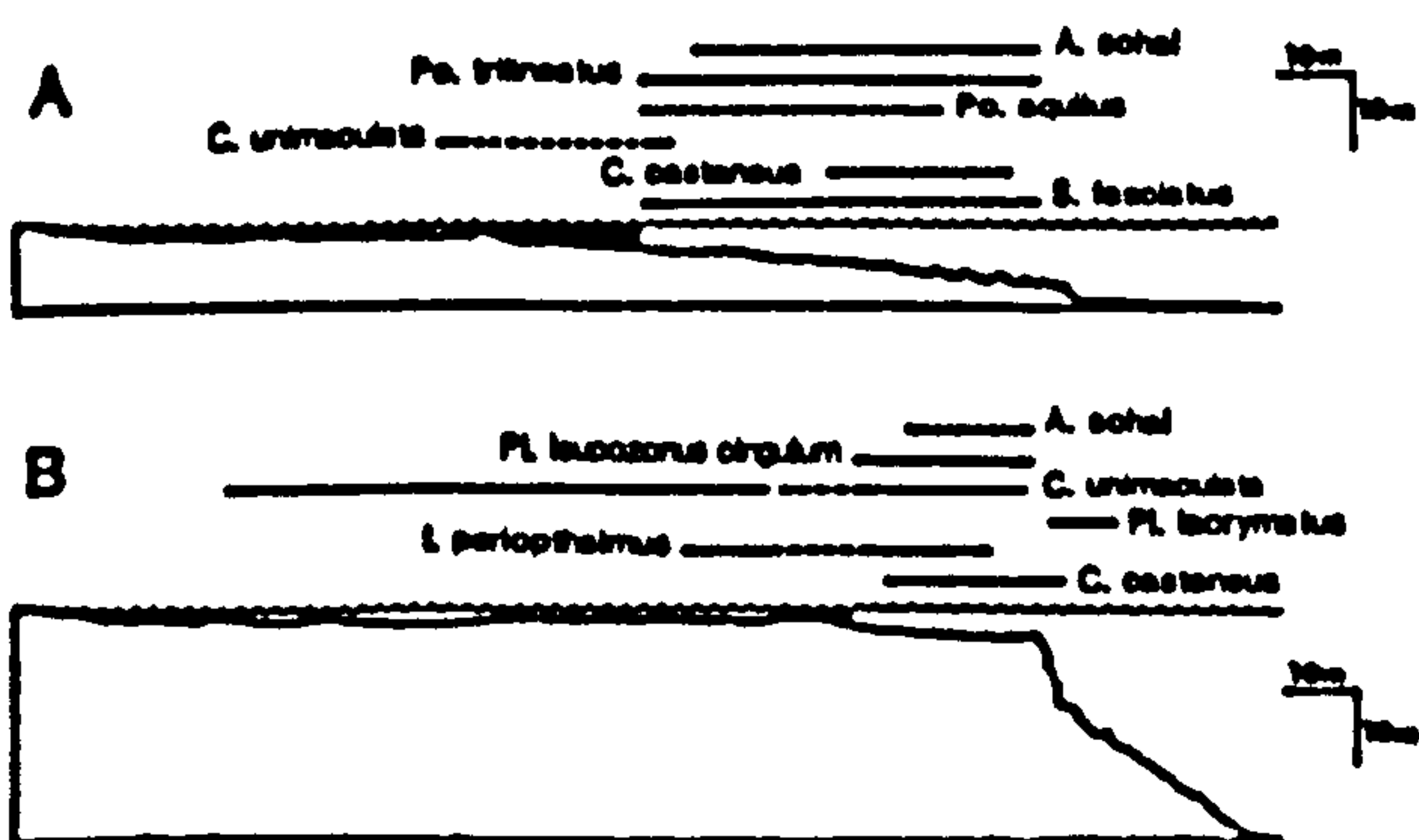


Figure 1: Distribution of study species and typical reef structure in (A) southern, and (B) northern Red Sea.

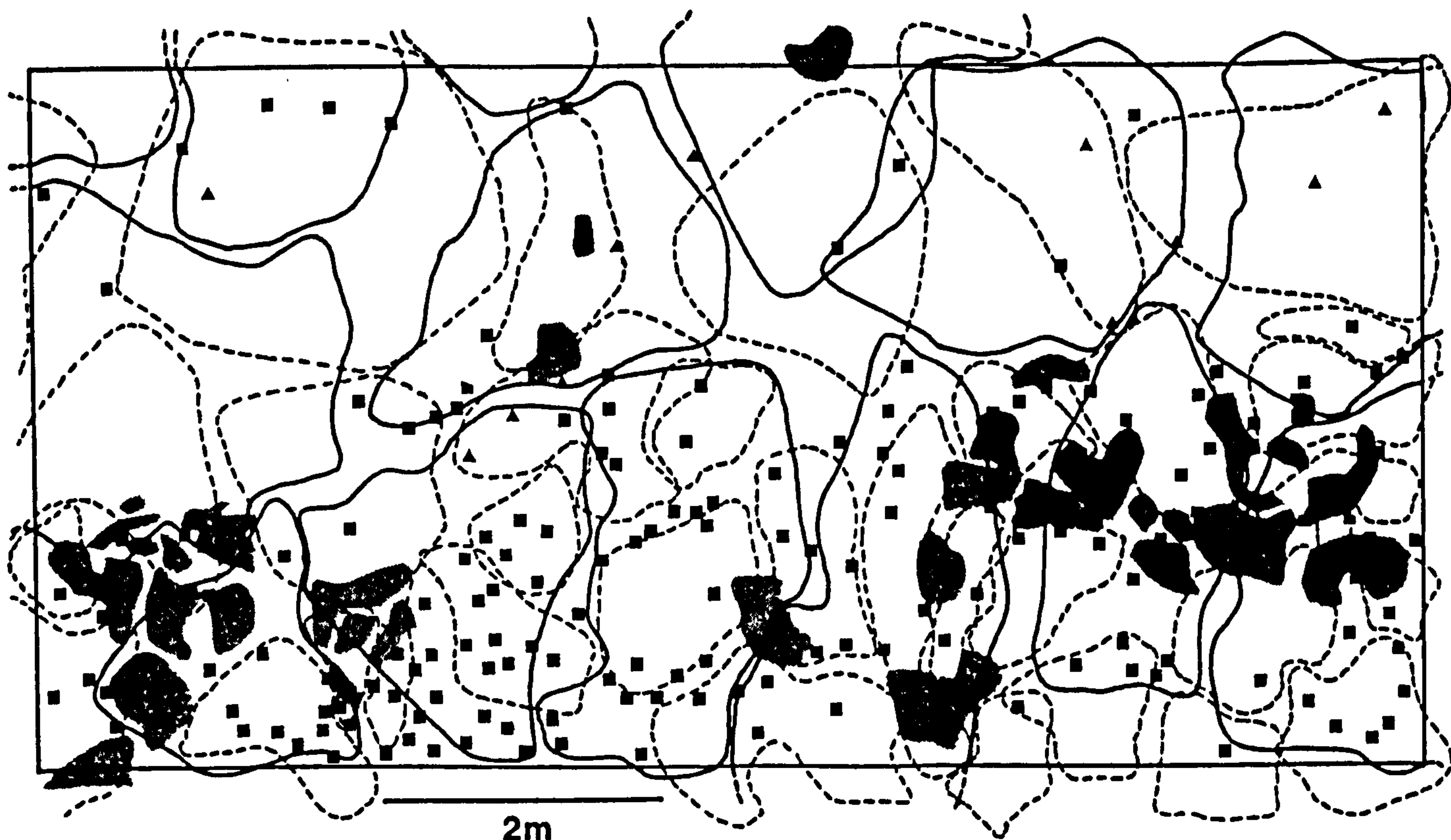


Figure 2: Territories of surgeonfish (*A. sohal*) and damselfish (*Pl. leucozonus cingulum* and *C. unimaculata*), and the positions of blenny refuge holes (one per individual) at the Jeddah site. Solid lines = surgeonfish; dashed lines = damselfish adults; shaded areas = damselfish juveniles; ■ = *Cirripectes castaneus* and ▲ = *Istiblennius periophthalmus*. The density of fish increases towards the reef-edge as the reef becomes more structurally complex. The quadrat measures 10 x 5m.

at the base of the reef-face (6-18m deep, Figure 1B).

Population structures

The damselfish and blenny species also hold territories outside *A. sohal* colonies. The densities and size structures of populations inside and outside *A. sohal* colonies, within the same reef zone, were assessed at the Jeddah site. Transect lines were laid through each area and the numbers, sizes (visually estimated length in cm) and species of individuals living within 1m either side of the line recorded. To do this the area was subdivided into 1m² quadrats and each was observed for five minutes. Individuals occupying two or more quadrats were only counted once. Populations from an area of 50m² within *A. sohal* colony areas and 55m² outside colonies were measured in this way. Data from areas occupied by *A. sohal* were pooled with data from the 50m² quadrat in which territories were mapped before analysis.

RESULTS

Territory overlap

Figure 2 shows territories of species from the central & northern Red Sea association at Jeddah. 71% of the area covered by surgeonfish territories within the quadrat overlaps with adult damselfish territories. This degree of overlap is not significantly different from a random distribution of territories of species of each family throughout the area ($\chi^2_1 = 0.01$, $p > 0.90$; the expected degree of overlap with random territory distribution is the product of the proportions of the quadrat covered by damselfish and surgeonfish territories). 72% of the area covered by juvenile damselfish territories lies within those of adult damselfish.

It is clear that *A. sohal* hold territories exclusive to conspecifics and adult damselfish hold territories exclusive to other adult damselfish. However, feeding areas of surgeonfish and damselfish overlap extensively. Juvenile damselfish territories are exclusive to other juveniles but overlap considerably with those of adults, most being situated along the edges of adult territories but with four completely contained within them.

Figure 2 shows a high degree of overlap of blenny feeding areas with those of damselfish and surgeonfish since blenny refuge holes always lie within the bounds of their territories. There is limited evidence of attempted exclusion of blennies by adult damselfish in that blenny refuge holes frequently lie on or close to the borders of damselfish territories.

Feeding habits

All of the species studied are primarily herbivores which browse predominantly on filamentous algae. Some animal material is also taken, probably ingested inadvertently whilst feeding on algae (Hiatt and Strasburg, 1960; Fishelson et al., 1974; Fricke, 1977). All species of damselfish in this study, particularly juveniles, were also observed to supplement their diet with zooplankton. Emery (1973) noted this ontogenetic shift in feeding habits in five species of territorial, herbivorous, Caribbean damselfish. Measurements of the feeding rates of species from both Red Sea associations indicate that all spend much time feeding on algae.

Defence of the algal lawn

Feeding rates of non-territorial herbivores within areas occupied by territorial fish are extremely low. Only one individual, a parrotfish (*Scarus psittacus*), was observed feeding during

SPECIES	No. of acts of aggression/15mins ($\bar{X} \pm$ S.D.)	Percentage of aggression interspecific	\bar{X} intensity of aggression towards conspecifics (\pm S.D.)	\bar{X} intensity of aggression towards heterospecifics (\pm S.D.)	Difference in intensity to conspecifics & heterospecifics. Mann-Whitney U-test.
<u>Southern Association</u>					
<u>A. sohal</u>	8.2 \pm 6.0	68	2.03 \pm 0.74	2.60 \pm 0.60	p << 0.001
<u>Po. trilineatus</u>	9.6 \pm 7.1	59	2.37 \pm 0.73	2.67 \pm 0.51	p << 0.001
<u>S. fasciatus</u>	1.3 \pm 1.8	27	2.03 \pm 0.85	1.90 \pm 0.57	NS
<u>Central & Northern Association</u>					
<u>A. sohal</u>	6.9 \pm 3.7	43	1.92 \pm 0.79	2.45 \pm 0.66	p << 0.001
<u>Pl. leuc. cingulum</u>	12.4 \pm 5.6	32	2.07 \pm 0.81	2.43 \pm 0.67	p << 0.001
<u>C. unimaculata</u>	8.6 \pm 4.6	47	1.62 \pm 0.76	1.80 \pm 0.77	p < 0.01
<u>C. castaneus</u>	0.9 \pm 1.6	24	2.43 \pm 0.79	2.55 \pm 0.73	NS
<u>Pl. lacrymatus</u>	10.1 \pm 4.4	88	1.96 \pm 0.81	2.79 \pm 0.45	p << 0.001

Table 2: Aggressive behaviour of the study species. NS = not significant.

the sixteen 30 minute observation periods. It was quickly chased by resident A. sohal as were 28 other fish during the observations (25 S. psittacus, 1 Hipposcarus harid & 2 Naso lituratus). Four individuals attempting to feed were also chased by resident Pl. leucozonus cingulum (3 S. psittacus & 1 N. lituratus). Feeding rates of herbivores in areas outside A. sohal colony areas were much higher with an average of 51.4 \pm 22.0 (S.D.) instances of feeding/30mins/m². Taken over the ten quadrats, 64% of these were due to parrotfish and 36% to surgeonfish. Defence of the algal lawn is thus very efficient.

Aggressive behaviour

Table 2 shows the average number of aggressive interactions/15 mins for each species. The data indicate that A. sohal and all species of damselfish invest heavily in territorial defence. Blennies are less overtly aggressive and appear to maintain territories more by display (Nursall, 1981).

Figure 3 shows the size distributions of heterospecifics aggressed against by surgeonfish and damselfish from both southern and central & northern associations. Damselfish exclude smaller individuals than do surgeonfish (Mann-Whitney U-test: A. sohal [south] vs Po. trilineatus, p << 0.001; A. sohal [central & north] vs Pl. leuc. cingulum, p << 0.001; A. sohal [central & north] vs C. unim-

aculata, p << 0.001).

Table 3 shows a breakdown by family of species aggressed against by territory holders from both associations. In both regions, A. sohal provides the majority of defence against larger herbivores, primarily scarids and siganids. Damselfish aggress against omnivorous and carnivorous fish (mostly labrids, chaetodontids, pomacanthids and serranids) more frequently than do A. sohal. The range of species aggressed against also tends to be greater in damselfish.

Plectroglyphidodon lacrymatus

Adults of this species occupy a different zone of the reef from A. sohal (Figure 1B). Figure 3 shows that Pl. lacrymatus aggress against large fish (> 20cm total length) more frequently than damselfish which share territories with A. sohal (C. unimaculata, $X_1^2 = 18.0$, p < 0.01; Pl. leucozonus cingulum, $X_1^2 = 7.3$, p < 0.02; Po. trilineatus, $X_1^2 = 12.8$, p < 0.01). Whilst aggressing at a similar frequency to damselfish species cohabiting with A. sohal (Table 2), a much higher proportion of these attacks were directed against heterospecifics (Pl. leuc. cingulum, $X_1^2 = 277.5$, p << 0.01; C. unimaculata, $X_1^2 = 170.8$, p << 0.01; Po. trilineatus, $X_1^2 = 101.5$, p << 0.01). Attacks on heterospecifics were also significantly more intense than in the other damselfish species and A. sohal (Mann-

FAMILY	Southern Association			Central and Northern Association				<u>Pl. lacrymatus</u>
	A.s.	Po.t.	S.f.	A.s.	Pl.l.c.	C.u.	C.c.	
Acanthuridae	102	1	0	201	23	5	0	13
Pomacentridae	16	449	10	34	406	275	2	134
Blenniidae	0	101	27	1	18	11	35	89
Scaridae	63	6	0	23	8	4	0	26
Siganidae	346	4	0	0	0	0	0	0
Labridae	3	147	0	9	18	42	0	125
Chaetodontidae	0	34	0	0	19	1	0	4
Pomacanthidae	2	0	0	0	2	0	0	7
Serranidae	0	1	0	0	2	1	0	8
Others	3	37	0	5	6	0	0	7
Number of species of heterospecific aggressed against	17	35	1	21	30	15	3	36

Table 3: Breakdown by family of species aggressed against by the study species. A.s. = A. sohal, Po.t. = Po. trilineatus, Pl.l.c. = Pl. leucozonus cingulum, C.u. = C. unimaculata, S.f. = S. fasciatus, C.c. = C. castaneus. Differences in the family composition of species aggressed against between regions reflect differences in the species composition of the fish communities between these regions.

SPECIES	Inside colonies	Outside colonies	Difference Mann-Whitney U-test
<u>Pl. l. cingulum</u>			
Size	6.7±2.7cm	4.0±2.4cm	p << 0.001
Density	0.7±1.8/m ²	0.8±0.7/m ²	NS
<u>C. unimaculata</u>			
Size	3.1±1.8cm	3.2±1.8cm	NS
Density	0.4±0.9/m ²	1.2±1.0/m ²	p << 0.001
<u>C. castaneus</u>			
Size	3.8±1.5cm	3.8±1.7cm	NS
Density	2.1±3.0/m ²	1.7±1.3/m ²	NS
<u>I. periopthalmus</u>			
Size	5.5±2.1cm	5.0±2.0cm	NS
Density	0.7±1.0/m ²	1.6±1.4/m ²	p << 0.001

Table 3: Population structures of damselfish and blennies inside and outside A. sohal colonies at Jeddah. Figures show mean and standard deviation.

Whitney U-test: Pl. leucozonus cingulum, p < 0.001; Po. trilineatus, p < 0.01; C. unimaculata, p << 0.001; A. sohal [central & north], p << 0.001; A. sohal [south], p < 0.01).

Population structure

Table 3 shows the average sizes of individuals and the population densities of damselfish and blennies inside and outside A. sohal colony areas at Jeddah. On average, Pl. leucozonus cingulum were significantly larger within A. sohal colony areas than in equivalent areas not occupied by A. sohal. This reflects a higher proportion of adults within and juveniles outside A. sohal colonies. The density of Pl. leucozonus cingulum did not differ significantly between areas. The average size of individuals in populations of C. unimaculata did not differ significantly but population density was greater in areas not occupied by A. sohal. Average sizes of both species of blenny did not differ significantly between areas, nor did the density of C. castaneus but I. periopthalmus was more common outside A. sohal colonies.

DISCUSSION

This study shows that in the Red Sea feeding territories are shared by herbivorous species of three families. In their study of territory sharing on Aldabra, Indian Ocean, Robertson and Polunin (1981) concluded that the damselfish Stegastes fasciatus was either a food parasite of surgeonfish, or that the relationship was commensal, the cost incurred by surgeonfish tolerating damselfish being little or nothing. The contribution to territory defence made by Red Sea damselfish appears considerably greater than that made by S. fasciatus (Robertson and Polunin, 1981). The average size of heterospecifics aggressed against is significantly smaller than those aggressed against by A. sohal so damselfish provide protection of the algal lawn from individuals not excluded by surgeonfish. The relationship between surgeonfish and damselfish hence may be mutualistic in the Red Sea.

That the damselfish benefit from the association is suggested by two observations: differences in population structure of species from the central & northern association at Jeddah outside and inside surgeonfish colonies, and territory defence behaviour by Pl. lacrymatus. Individuals of Pl. leucozonus cingulum are significantly larger within areas occupied by A. sohal than outside. Pl. leucozonus cingulum is aggressively dominant to the smaller C. unimaculata and the density of the latter is significantly lower in areas occupied by

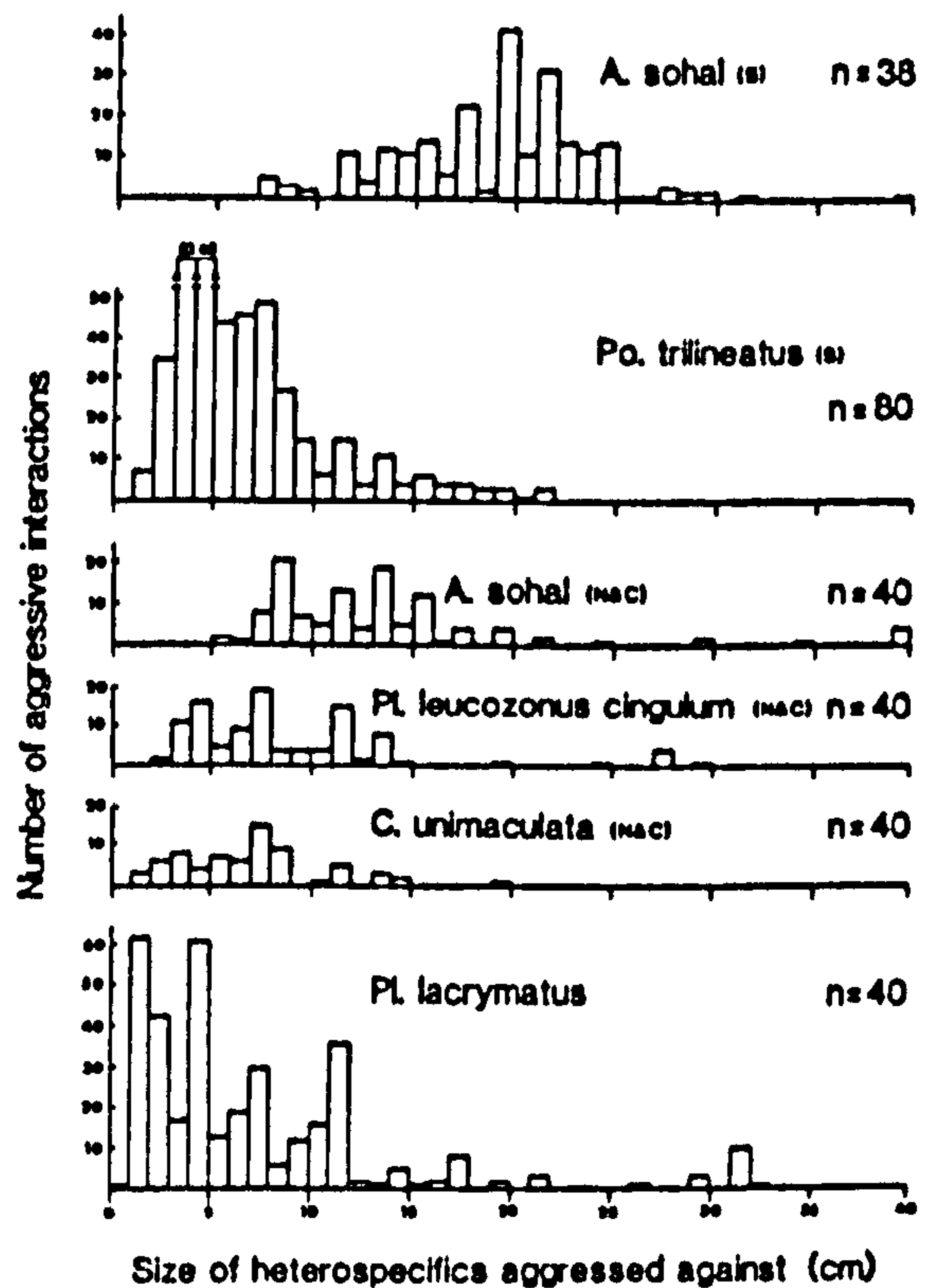


Figure 3: Sizes of heterospecifics aggressed against by the study species. Sizes were estimated.

A. sohal than outside, suggesting that Pl. leucozonus cingulum partially excludes them from such areas. The evidence implies that A. sohal colonies are preferred by Pl. leucozonus cingulum over other areas. The study of Pl. lacrymatus also indicates the benefit of A. sohal to cohabitant damselfish. Levels of interspecific aggression are much higher in Pl. lacrymatus than in damselfish cohabitant with A. sohal (compensated for by a reduction in intraspecific aggression), and a wider size range of individuals are aggressed against.

Robertson and Polunin (1981) suggest four reasons for surgeonfish tolerating damselfish: (1) damselfish contribute to interspecific defence of the algal lawn and so are beneficial, (2) the impact of damselfish on the algal lawn is low since they have a low biomass density compared to surgeonfish, (3) they would be difficult to exclude as they retreat into refuge holes when aggressed against, and (4) damselfish might be feeding on different resources from surgeonfish. This study suggests that the association is mutualistic and that (1) is of primary importance. (2) and (3) probably also have considerable importance. I know of no instances of territory sharing between similarly sized reef fish species feeding on the same food. (4) has not been explored in this study but is unlikely to be important. This is because it is improbable that damselfish feed on different species of algae from A. sohal since algal species are intermixed in the algal lawn at a scale much smaller than these fish's mouths (Hatcher, 1983). Robertson and Polunin (1981) investigated the possibility that cohabitants fed from different microhabitats within areas of territory overlap but found little evidence of such separation.

Territory sharing between damselfish and surgeonfish in the Red Sea is analogous to territory sharing in terrestrial communities between owners and satellites, for example in birds (Davies and

Houston, 1981). However, unlike the case in most terrestrial associations, the satellites are not of the same species and surgeonfish appear not to have the option of excluding them, i.e. damselfish.

Blennies contribute nothing to interspecific defence of the algal lawn and assuming, as above, that they are not feeding on different resources, are food parasites of surgeonfish and damselfish. They are tolerated (although not by Po. trilineatus) probably because the cost of their exclusion would be very high. Like damselfish, blennies have refuge holes into which they will dart at the approach of an aggressor. The aggression by Po. trilineatus towards S. fasciatus does not result in their exclusion. However, it may reduce their density within territories, as observed by Low (1971) in territories of Pomacentrus flavicauda on the Great Barrier Reef. Figure 2 shows limited evidence of adult damselfishes affecting the distribution of blennies but this is equivocal and is somewhat contradictory to observational evidence of a very low frequency of attacks directed at C. castaneus by Pl. leucozonus cingulum and C. unimaculata.

Juvenile damselfish (< 3cm total length) are also food parasites of surgeonfish and adult damselfish but to a lesser extent than blennies since they supplement their diet with zooplankton. They contribute nothing to interspecific defence of the algal lawn (Roberts, unpublished data) and their territories overlap considerably with those of adult damselfish and surgeonfish (but little with those of other juveniles). Sale et al. (1980) have discussed recruitment strategies of juvenile damselfish and note their use of topographic features to avoid exclusion by adults. Like adults, they would be very costly to exclude since they retreat into refuge holes when aggressed against. The balance between the cost of tolerating a juvenile and excluding it will shift as the juvenile grows, exclusion progressively becoming more viable.

Territory sharing by herbivorous reef fishes is widespread (Robertson and Polunin, 1981) but the mechanisms by which coexistence is maintained differ. In their study, Robertson and Polunin (1981) found that the territories of S. fasciatus were aggregated within those of surgeonfish. In contrast, the present study shows that territories of damselfish and surgeonfish in the Red Sea are distributed at random with respect to each other at a fine spatial scale. Robertson (1984) has described a very similar system of territory sharing to that found in the Red Sea but where the role of the surgeonfish is assumed by a large damselfish, Microspathodon chrysurus. M. chrysurus shares the territories of two species of smaller damselfish and one species of blenny through competitive dominance. Sharing of territories by damselfish and blennies has not to my knowledge been studied. Nursall (1981) and Robertson (1984) note that territories of the Caribbean blenny Ophioblennius atlanticus are often shared with damselfish, and Low's (1971) data suggest territory sharing by blennies and a damselfish on the Great Barrier Reef. Clearly, territory sharing represents a means by which some part of the high within-habitat diversity of coral reef fish assemblages is maintained.

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ADDITIONAL NOTE

An experiment was performed in order to assess the effects of territorial, herbivorous surgeonfish (Acanthurus sohal) and damselfish (Plectroglyphidodon leucozonus cingulum and Chrysiptera unimaculata) on algal standing crop and growth rates at the Jeddah site discussed in the preceding paper. Ten concrete paving slab fragments were submerged within areas occupied by A. sohal and ten in areas not occupied by A. sohal (referred to as coralline algal areas). The two groups were separated by approximately 30m and slabs spread randomly throughout each with the restriction that they should be approximately horizontal. Slabs within areas occupied by territorial herbivores rapidly developed algal communities and these became superficially indistinguishable from the surrounding algal lawn within a period of four weeks. Algal colonisation of slabs within coralline algal areas was much slower. After 34 days, five slabs were raised from within the area occupied by A. sohal, and after 38 days nine of the slabs from within the coralline algal area were raised (one had been washed away by wave surge). Algae were scraped from each slab, dried and sealed in plastic bags. The outline of each slab was traced and kept with the algae from the same slab. The surface areas from which the algae were scraped were later calculated from these outlines. The ash-free dry weight of each sample was calculated on return to the United Kingdom. The results are shown in Table A. Areas occupied by A. sohal had an algal standing crop on average around ten times greater than coralline algal areas. Thus the territorial activities of A. sohal and cohabitant damselfish result in a marked increase in algal standing crop over surrounding areas.

The remaining five slabs within areas occupied by territorial herbivores formed the basis of a caging experiment, the aim of which was to estimate algal growth rates and fish grazing pressure. Five cages were made of 7mm wire mesh, each measuring 30 x 30 x 10cm. These were tied to the substratum next to each of the slabs (48 days after they were first submerged). Each of these slabs was broken into three: one piece was removed and scraped as above, one piece was placed inside the cage and the cage wired shut, and one piece was left next to the cage and exposed to fish grazing. Cage mesh size was such that only the smallest herbivorous blennies would be able to gain access to the caged slabs. Seven days later, all ten fragments were removed from the water and algae scraped from them as above. The results are shown in Table A. The short duration of the experiment meant that growth rates of algae within cages were not reduced by light reduction by fouling organisms.

Algal standing crop on caged slabs increased over uncaged slabs by approximately 3-4 times during the week. This increase represents both the algal growth rate (productivity) and the grazing pressure by fishes since standing crops on uncaged slabs between the beginning and

the end of the week were very similar.

These data were to form a basis for estimation of the energetics of territory sharing by surgeonfish, damselfish and blennies. However, there was insufficient field-time for the necessary behavioural and gut content studies needed to supplement this information.

<u>TREATMENT</u>	MEAN AFDWg/m ² (<u>±</u> S.D.)	<u>N</u>
34 days submerged in <u>A. sohal</u> areas	19.11 <u>±</u> 14.27g	5
38 days submerged in coralline algal area	2.08 <u>±</u> 1.19g	9
Caging Experiment:		
Raised at start	9.59 <u>±</u> 1.48g	5
Outside cage	11.12 <u>±</u> 1.54g	5
Inside cage	35.00 <u>±</u> 13.36g	5

Table A: Results of the experiment involving algal settlement on concrete slabs at a site near Jeddah, Saudi Arabia. AFDW = ash-free dry weight.

Chapter 6

**Experimental analysis of resource sharing
between herbivorous damselfish and blennies
on the Great Barrier Reef.**

ABSTRACT

Niche theory suggests that species with very similar resource requirements should not be able to coexist. However, on coral reefs, territorial herbivorous fishes which use apparently very similar resources often coexist without competitive exclusion. This study investigates patterns of resource use by damselfish (Pomacentrus flavicauda) and blennies, primarily Salarius fasciatus, living in rubble habitats on the Great Barrier Reef. These species feed mainly on turf algae and have overlapping territories and home-ranges. I ask two questions: (1) is there any evidence of resource partitioning between these species, and (2) do they compete for food? It is highly unlikely that damselfish and blenny species partition food resources by eating different species of algae, since species are intermixed at a very small scale in the algal turf. Instead, differences in food use were looked for by counting the numbers of bites fish of each species took from different parts of the rubble habitat. Little difference in food use was found between P. flavicauda and S. fasciatus except that the former fed on plankton to some extent whilst the latter did not. A manipulation experiment was performed to assess whether blennies inhabiting damselfish territories competed with damselfish for algae. Damselfish territories were used as experimental units and two manipulations performed: (1) S. fasciatus removal, and (2) P. flavicauda removal. There were four replicates of each with four undisturbed controls. Territory sizes, feeding rates and attack rates on other fish of P. flavicauda were measured before and after blenny removal. Blenny density and biomass were measured before and after P. flavicauda removal. None of these measures provided evidence of exploitation competition between these species or of changes in levels of interference competition by damselfish after blenny removal. Blenny densities and biomass did not change significantly after damselfish removal. Damselfish appear to tolerate blennies within their territories because they cannot economically exclude them. However, the intermittent availability of an alternative source of algae outside damselfish and blenny territories and home-ranges may mean that algae is not normally a limiting resource.

INTRODUCTION

During the past decade or so there has been much controversy over the role of competition in structuring ecological communities (Strong et al., 1984; Simberloff, 1982). The principle of competitive exclusion states that under conditions where some resource(s) is limiting, species using this resource(s) in a similar way should not be able to coexist (Abrams, 1983). Thus species within communities have been assumed to coexist through competitively driven niche differentiation (MacArthur, 1965). This view has been particularly intensely disputed in the field of coral reef fish ecology. Sale (1974) found that in a guild of territorial herbivorous damselfish, patterns of resource use were very similar between species. All fed predominantly on filamentous algae and there was much overlap in use of space by many species. Sale generalised these findings to the whole coral reef fish community, suggesting that for most species space was a limiting resource (Sale, 1978). High species diversity is maintained by random recruitment of competitively 'equal' species to fill unpredictably available space (Sale, 1979). Any given 'space' (created usually by the death of the former occupant) may be filled by one of many species. Hence, coexistence between species is mediated not by resource partitioning but through stochastic processes preventing competitive exclusion (Sale, 1978). However, others argue that coexistence between species on coral reefs can be explained by the conventional dogma of resource partitioning (Smith and Tyler, 1972; Robertson and Lassig, 1980; Waldner and Robertson, 1980; Anderson et al., 1981; Gladfelter and Johnson, 1983).

Like resource partitioning theory, Sale's lottery hypothesis requires that species with very similar resource requirements do not locally use the same resources. However, this is achieved through individuals of such species maintaining mutually exclusive territories: competitive exclusion at a small scale. Interspecific territorial defence is well documented amongst coral reef fish, particularly herbivorous species (Low, 1971; Myrberg and Thresher, 1974). Species with similar resource requirements are excluded whilst others are tolerated (Thresher, 1978; Moran and Sale, 1977; Losey, 1982). However, this is not always the case. Robertson and Polunin (1981), Robertson (1984) and Roberts (1985) have documented patterns of territory sharing by interspecifically territorial damselfish and surgeonfish. In two cases, territories of larger surgeonfish and in one case of a larger damselfish overlap with those of smaller damselfish. All species feed on the filamentous algal turf which grows within their territories. Robertson and Polunin (1981) argue that the larger surgeonfish tolerate damselfish because: (1) damselfish contribute to territory defence, (2) they have little impact on the algal turf since their biomass density is low compared to surgeonfish, and (3) they would be energetically costly to exclude because they

dart into refuge holes when aggressed against. Size differences between these coexisting species seem critical to coexistence (Roberts, 1985). However, this widespread phenomenon is further complicated by herbivorous blennies also sharing the territories of damselfish and surgeonfish and feeding on the algal turf (Nursall, 1981; Robertson, 1984; Roberts, 1985). Unlike damselfish and surgeonfish, these blennies contribute little to interspecific defence of the algal turf against other herbivores (Roberts, 1985). They are also usually present in high densities and their impact on this algal turf cannot be dismissed as being insignificant. In fact, Hatcher (1981) and Walker (1984) found that blennies are, in terms of grazing pressure, probably the most important grazers on the algal turf. There are thus grounds for believing that competition between blennies and cohabitant damselfish and surgeonfish may be intense. Many species of blenny cohabitant with damselfish are similar in size to these damselfish. How do they coexist? This study investigates patterns of space and food use by damselfish and blennies which coexist within rubble habitats within the Great Barrier Reef. Two questions are addressed: (1) do these species compete for food or space, and (2) is there any evidence of resource partitioning between them which may explain coexistence?

METHODS AND STUDY AREA

Study area and species

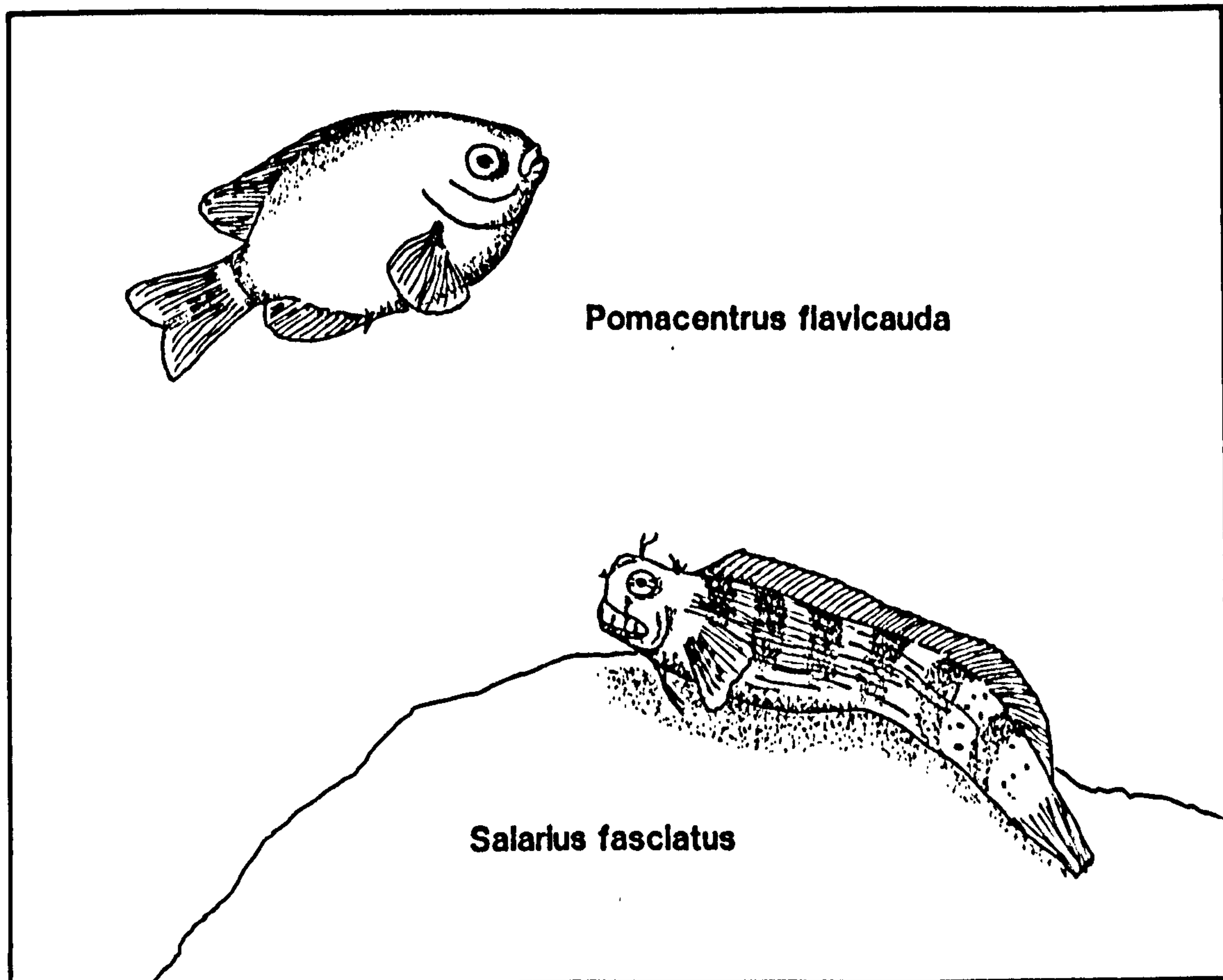
This study was conducted on One Tree Reef at the southern end of the Great Barrier Reef during July and August of 1985. Interactions between the damselfish Pomacentrus flavicauda and the blenny Salarius fasciatus (Figure 1) were studied in populations inhabiting the rubble slope which forms the eastern edge of the lagoon (Figure 2). This rubble bank drops steeply from the ponded lagoon water level to a sand bottom at 1.5 - 2m deep. Individuals of Pomacentrus flavicauda hold interspecifically defended territories which overlap with the home-ranges and territories of S. fasciatus. Both these species feed primarily on the filamentous algae which form a thin turf over much of the hard substratum on the rubble bank. Adult P. flavicauda reach up to 8cm long whilst S. fasciatus grow up to 11cm long. The ecology of P. flavicauda has been described in detail elsewhere (Low, 1971; Doherty, 1983). Three other species of herbivorous blenny are also common in the study area: Atrosalarius fuscus, Ecsenius mandibularis and Istiblennius edentulus. The latter species is primarily an inhabitant of a narrow fringe at the top of the rubble bank, immediately below the low water mark. Movements of I. edentulus overlap little with those of P. flavicauda since P. flavicauda territories are usually situated in the lower and middle regions of the rubble bank. A. fuscus and E. mandibularis are found within P. flavicauda territories but are considerably smaller than S. fasciatus and occur at lower densities.

Feeding microhabitats

P. flavicauda and S. fasciatus may coexist through partitioning of food resources. This could be either through selection of different foods, or by feeding on the same foods but from different parts of the areas in which they cohabit. In order to test the latter, eleven different feeding microhabitats were defined, such as 'small crevice' and 'exposed concavity', after the method of Robertson and Polunin (1981). The numbers of bites of food which individuals took from each were counted within timed periods. Thirteen P. flavicauda were observed for 60 minutes each and twenty-five S. fasciatus observed for 30 minutes each. Differences in the mean proportions of bites taken by each species from each microhabitat were tested for using the Mann-Whitney U-test.

Experimental methods

Competition for food between P. flavicauda and blennies, primarily S. fasciatus, was tested for in a removal experiment. The



Pomacentrus flavicauda

Salaria fasciatus

Figure 1: Two of the study species.

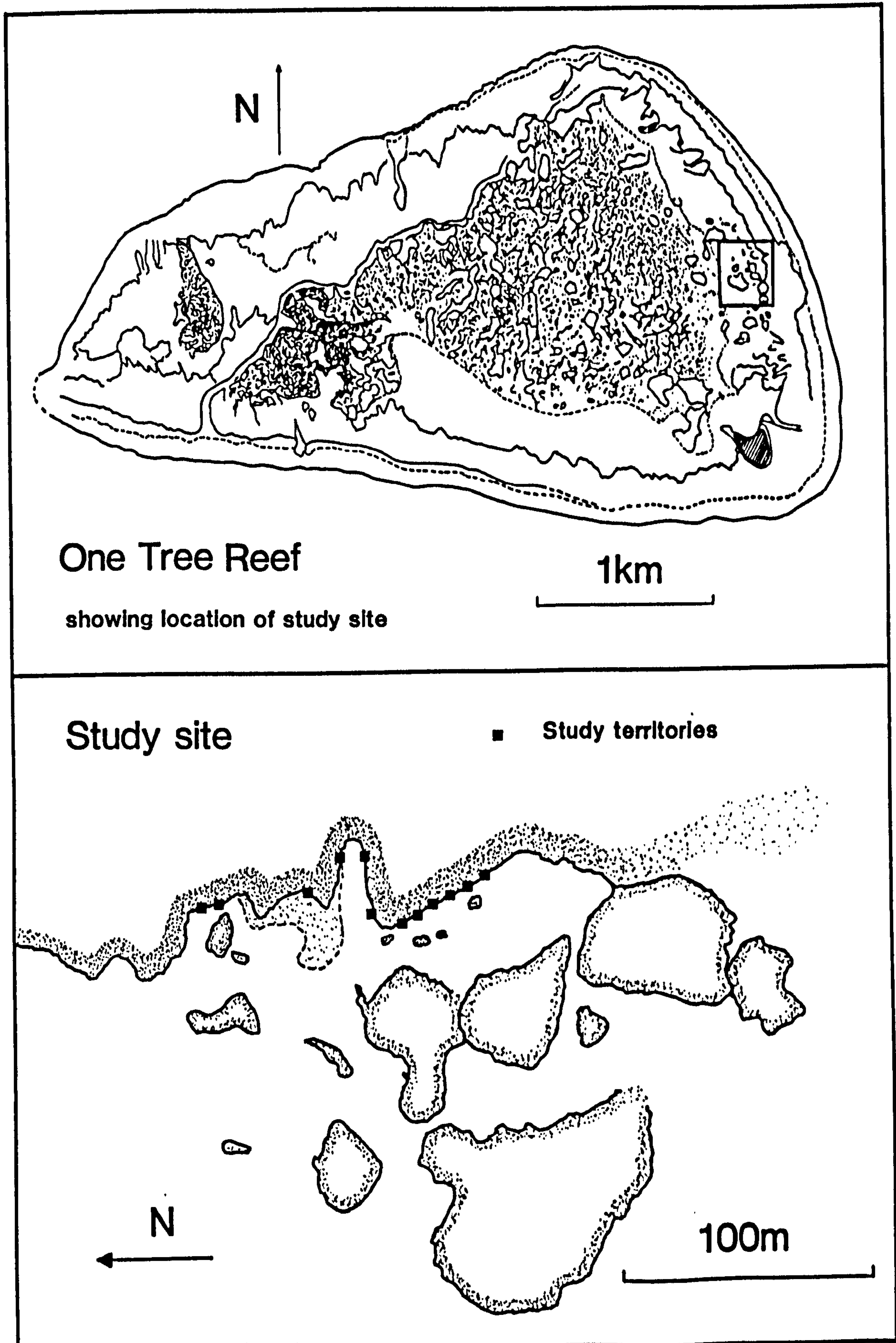


Figure 2: Map of One Tree Reef showing the locations of the study site and the territories of the damselfish *Pomacentrus flavicauda* which formed the focus of the study.

territories of individual damselfish were used as experimental units and manipulations were centred on these. Twelve territories were selected and these were separated from experimental territories by distances of at least five metres (Figure 2). Sketch maps were drawn of the rubble bank in the area of each territory.

Two manipulations were performed. S. fasciatus and I. edentulus were removed from four of the damselfish territories, and the damselfish were removed from another four. E. mandibularis and A. fuscus were not removed since their impact on the algal turf is likely to be low compared with S. fasciatus due to their small sizes and low densities. Four territories were left undisturbed as controls. Treatments were assigned to territories randomly. Damselfish were removed by spearing and blennies using the anaesthetic quinaldine.

Several measurements were made on the experimental and control units before and after the manipulations. P. flavicauda territory sizes were measured by watching each individual for a set period and plotting its location on the sketch map of the area at ten second intervals. In addition, the locations of all aggressive encounters with other fish during this period were noted. Territory areas were calculated using the convex polygon method (Odum and Kuenzler, 1955), the outermost localities visited being joined such that the resulting polygon has no concavities.

In order to determine the minimum period adequate to map the territories of P. flavicauda graphs of cumulative territory area versus duration of observations were plotted for a sample of individuals. The minimum mapping period is taken as the time after which continued observations result in only a 5% increase in perceived territory area (Odum and Kuenzler, 1955). The mean length of observation period at which this point was reached was 39 ± 19 minutes (95% C.I., $n = 20$). A 60 minute observation period was chosen to give an accurate measure of territory size for most fish.

The feeding rates of P. flavicauda (numbers of bites taken in 60 minutes) and the numbers of aggressive encounters with other fish (during 60 minutes) were also measured on blenny removal and control units before and after manipulations.

Densities of herbivorous blennies were measured by repeated census before and after manipulations on all twelve units. Each P. flavicauda territory was observed for 30 minutes and the locations and lengths (estimated to the nearest half centimetre) of each blenny noted. Blennies usually move in discrete steps from rock to rock and such movements of most individuals were recorded at each census. Two censuses were made before manipulations and three after. A length-weight relationship (weight = constant \times length³, Jones and Chase [1968]) was calculated for S. fasciatus using individuals removed during manipulations. Hence the biomass density of S. fasciatus within each damselfish territory could also be estimated at each census.

The data were analysed using a two-way ANOVA with repeated

measures, the repeated measures being those variables measured before and after manipulation.

RESULTS

Figure 3 shows the overlap in space use between P. flavicauda and S. fasciatus. This diagram shows the pattern of space use from only one P. flavicauda territory but is typical of patterns observed from all the other territories, although at some other sites there is a greater degree of overlap between neighbouring S. fasciatus. S. fasciatus were present within P. flavicauda territories at an average density of 2.2 ± 0.86 (S.D.)/m², whilst the other common blennies, E. mandibularis and A. fuscus were present at densities of 0.42 ± 0.65 (S.D.)/m² and 0.15 ± 0.18 (S.D.)/m² respectively.

Frequencies of attacks on other fish were high in both P. flavicauda and S. fasciatus with 10.2 ± 5.6 (S.D.) attacks/30 mins and 5.5 ± 3.9 (S.D.) attacks/30 mins respectively (n = 34 in both cases). Table 1 shows a breakdown of the subjects of attacks by these species. Levels of intraspecific aggression were low in P. flavicauda but high in S. fasciatus. However, these low levels of intraspecific aggression in P. flavicauda were probably primarily a result of the relatively low density of this species, most territories not being contiguous with those of conspecifics. 11.4% of interspecific attacks by P. flavicauda were directed against S. fasciatus, 2.9% against E. mandibularis, 2.3% against A. fuscus and 1.3% against I. edentulus. 14.5% of interspecific attacks by S. fasciatus were directed against P. flavicauda. However, this aggression failed to secure individuals of either species exclusive use of an area.

Whilst all individuals of P. flavicauda are interspecifically territorial, only a small proportion of individuals of S. fasciatus appear to be so. Figure 4 shows the population size structure of S. fasciatus inhabiting P. flavicauda territories. Only a small number of the largest individuals (8-10cm) were observed to be interspecifically territorial. Other individuals (from 2-10cm) either held intraspecifically defended territories or had overlapping home-ranges with size-related dominance between individuals. Unlike P. flavicauda in which a large proportion of interspecific attacks were directed against individuals simply trespassing within the territory but not feeding, interspecific attacks by S. fasciatus were almost always elicited by intruding individuals actually feeding. The blenny would swim to where the individual(s) was feeding and force it to move on by displacement, this sometimes happening several times before the individual(s) left the territory. Only rarely would individuals be chased, whilst P. flavicauda almost always chased trespassers.

Feeding rates of P. flavicauda and S. fasciatus on the filamentous algal turf were high. On average P. flavicauda took 98.9 ± 42.5 (S.D.) bites/30mins (n = 34), whilst S. fasciatus took 225.6 ± 92.6 (S.D.) bites/30 mins (n = 30). Assuming that feeding rates are constant throughout the day then, at the average densities of individuals observed, S. fasciatus take 9,926 bites/m²/day and P.

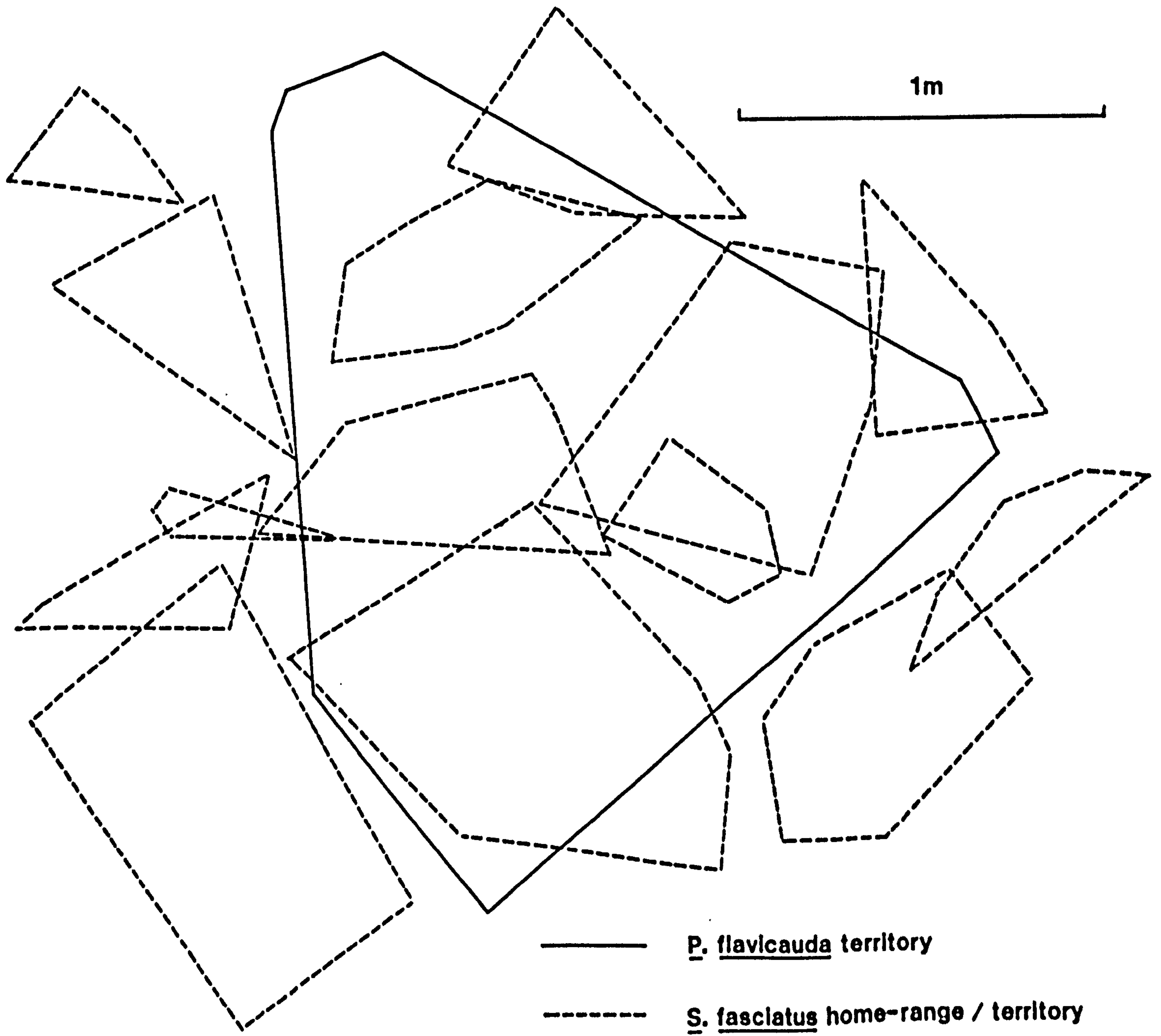


Figure 3: Overlap in space use between *P. flavicauda* and *S. fasciatus* from one of the experimental units.

	<u>P. flavicauda</u>	<u>S. fasciatus</u>
Intraspecific	15	136
Interspecific:		
Pomacentridae	115	9
Blenniidae	74	12
Scaridae	57	24
Labridae	32	4
Chaetodontidae	10	0
Gobiidae	9	2
Clinidae	2	0
Tripterygiidae	1	2
Tetraodontidae	1	0
Clupeidae	1	0
Pseudochromidae	1	0
Synodontidae	1	0
Parapercidae	1	0
Eleotrididae	0	2
Total	320	191

Table 1: Breakdown by family of species attacked by Pomacentrus flavicauda and Salarius fasciatus. Data are from 34 individuals of each species observed for 30 minutes each. Figures shown represent the total numbers of attacks on species from each family during the total observation period.

FEEDING MICROHABITAT	<u>P. flavicauda</u>	<u>S. fasciatus</u>	SIGNIFICANCE
Exposed flat horizontal	0.10	0.11	NS
Exposed flat vertical	0.10	0.15	P < 0.05
Exposed concavity	0.20	0.21	NS
Exposed convexity	0.27	0.33	NS
Large crevice	0.07	0.06	NS
Small crevice	0.08	0.08	NS
Entrance of small cave	0.03	0.03	NS
Inside small cave	0.02	0.02	NS
On sand	0.003	0.00	NS
Plankton	0.12	0.002	P < 0.01
Robbing other fish	0.003	0.00	NS

Table 2: Mean proportions of bites taken from different microhabitats by P. flavicauda and S. fasciatus. Differences tested for using the Mann-Whitney U-test. Data are from 13 P. flavicauda observed for 60 minutes each and 25 S. fasciatus observed for 30 minutes each.

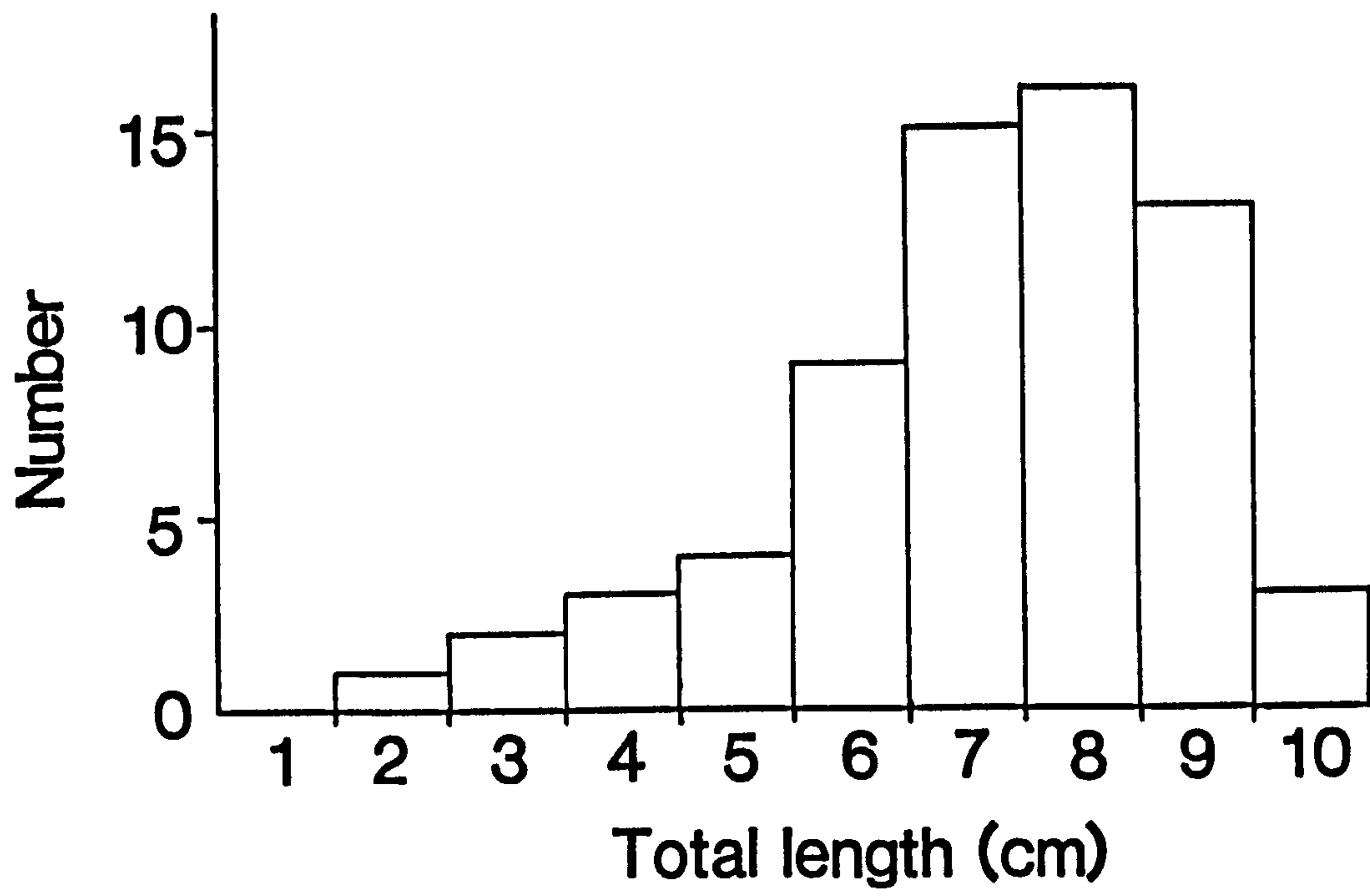


Figure 4: Population size structure of *S. fasciatus* inhabiting *P. flavicauda* territories at the study site.

flavicauda 755 bites/m²/day (during the 10 hours of daylight available for feeding in the period July to August). As an approximation I assume that each bite removes the algae from an area of 0.15cm² of substratum. Thus S. fasciatus remove algae from 14.9% of the area per day compared with only 1.1% for P. flavicauda. However, cover of algae bearing substratum is probably only around 50 - 75% within P. flavicauda territories and so these figures are underestimates of the actual amounts of available algae removed. However, they indicate that S. fasciatus eat around 13-14 times as much of the available algae as P. flavicauda, assuming equal feeding efficiency.

In order to assess whether damselfish and blennies differ in their use of food resources, counts were made of the number of bites taken by each species from each of nine different substratum-based microhabitats. In addition, fish were sometimes observed feeding on plankton or suspended particulate matter, or robbing food from other fish, and so bites from these sources were also recorded. Table 2 shows the results and indicates that the mean proportions of bites from each source differ significantly between species in only two cases. S. fasciatus take more bites from exposed, flat, vertical surfaces than do P. flavicauda, and P. flavicauda feed on plankton whilst S. fasciatus do not.

After all preliminary observations were completed, manipulations were performed on the study units over a period of two days. Four P. flavicauda were removed from their territories and S. fasciatus were removed from a further four P. flavicauda territories. Where other P. flavicauda expanded contiguous territories to overlap the areas formerly occupied by experimental fish, these were also removed. Two further individuals were removed for this reason. S. fasciatus removed were, for a time, rapidly replaced by others (at one site by I. edentulus). Whilst only thirty-one S. fasciatus were observed on territories earmarked for blenny removals prior to manipulations, seventy-one were removed from these and their immediate surrounds. Eleven I. edentulus were also removed from one territory. Manipulations were successful in reducing the biomass of S. fasciatus within P. flavicauda territories by 70-80% during the period in which post-manipulation observations were made.

Many cost/benefit models of territoriality assume that the optimum territory size is the minimum possible to support the needs of the fish (Ebersole, 1980; Hixon, 1980; Davies and Houston, 1984). If blennies are competing with damselfish for algae then you might expect damselfish territories to contract after blennies have been removed. However, territory size need not be a very precise indicator of whether species are competing or not. Since there are only three possible responses to a manipulation (increase, decrease or no change in size), agreement between expectation and reality may be purely fortuitous (M.A. Hixon, pers. comm.). For this reason, time-budget measurements of feeding rates and attack rates on other fish were also

made. If blennies interfere with damselfish feeding then you might expect damselfish feeding rates to increase after blenny removal, or numbers of aggressive interactions to decrease.

Table 3 shows the average values of each of the measures made on experimental and control units before and after manipulations were performed. These data were analysed using a two-way ANOVA with repeated measures. There are three components to this ANOVA: the group effect, being experimental versus control units; the fish effect, being differences between individual replicates; and the event effect, being the change in any measure between before and after manipulation. If the experimental group are affected by the manipulation, then experimental and control groups should respond differently over the timecourse of the experiment. This would be indicated by a significant group-event interaction. None of the group event interaction terms was significant for any of the measures in the case of either blenny removal or damselfish removal treatments. The manipulations thus appear to have had no significant effect on the behaviour of either P. flavicauda or S. fasciatus and hence this experiment has failed to detect evidence of competition for food between these species.

There was one significant group effect. Experimental P. flavicauda territories were, on average, larger than control territories both before and after blenny removals ($P < 0.05$, Table 3). However, this should not affect the conclusions of the experiment. In addition, there was a significant event effect for damselfish feeding rate ($P < 0.01$), feeding rates being higher on both experimental and control territories after blenny removal. Hatcher (1981) found a strong correlation between water temperature and herbivore feeding rates. On the flood tide, water entering the lagoon was 2-3 °C warmer than water which had been standing within the ponded lagoon (this water having been cooled by wind-driven evaporation). Differences in tidal state between pre- and post-manipulation observations probably account for the increase in feeding rates.

<u>TREATMENT</u>	<u>MEASURE</u>	<u>GROUP</u>	<u>BEFORE</u>	<u>AFTER</u>
<u>S. fasciatus</u> removal	<u>P. flavicauda</u> territory size (m ²)	Exp.	3.0 ± 0.3	3.4 ± 0.3
		Control	2.2 ± 0.3	2.3 ± 0.1
	<u>P. flavicauda</u> feeding rate (bites/15mins)	Exp.	177.3 ± 42.1	254.7 ± 27.2
		Control	100.5 ± 31.9	176.7 ± 23.7
<u>P. flavicauda</u> removal	<u>P. flavicauda</u> acts of aggression (per 15mins)	Exp.	15.2 ± 3.0	18.2 ± 2.3
		Control	18.2 ± 2.2	26.0 ± 9.3
<u>P. flavicauda</u> removal	<u>S. fasciatus</u> density (no. per territory)	Exp.	6.0 ± 1.9	6.5 ± 2.0
		Control	4.7 ± 0.8	5.1 ± 0.6
	<u>S. fasciatus</u> biomass (g/ <u>P. flavicauda</u> territory)	Exp.	23.8 ± 3.7	29.1 ± 5.2
		Control	21.0 ± 6.7	21.1 ± 7.2

Table 3: Average values (± standard error) of each of the measures used in the two-way ANOVA with repeated measures, before and after the manipulations were performed.

DISCUSSION

In a study on the nearby Heron Island, Low (1971) found that the densities of S. fasciatus increased within the territories of P. flavicauda after removal of these territory holders. This suggests that P. flavicauda attempt to depress the densities of S. fasciatus within their territories, suggesting competition between these species. However, this result was not found in the present study. Densities and patterns of space use in S. fasciatus overlapping P. flavicauda territories remained stable after removal of the damselfish. Additionally, changes in territory size and feeding rates of P. flavicauda gave no indication of exploitation competition with S. fasciatus. Neither did changes in attack rates after blenny removal suggest a reduction in effort invested in interference competition.

If damselfish and blennies do compete for food in rubble habitats of One Tree Reef, then why has this experiment failed to detect such competition? The low numbers of replicates in each treatment will mean that the experiment had limited power, resulting in a reasonably high chance of making a Type II error (failing to reject a false null hypothesis). However, if we accept the results of this experiment, then why might these species not be competing when their space and food requirements seem so similar?

The feeding microhabitat study showed little evidence of partitioning of the algal resource within areas of overlap. However, this does not preclude the possibility that damselfish and blennies are selecting different species of algae. Selectivity of algal species by fish has been shown for fish feeding on macro-algae (Lobel, 1980; Littler et al., 1983; Hay, 1985; Lewis, 1985; Wolf, 1985). However, intermediate to high levels of grazing intensity favour the growth of turf algae and coralline algae (Hixon and Brostoff, 1983; Littler and Littler, 1985) and these dominate in the rubble habitats of One Tree Reef, there being virtually no macro-algae at all at the study site. There are over 180 species of algae in the Capricorn Group of the Great Barrier Reef, of which One Tree Reef is a part (Borowitzka, 1981). Hatcher (1983) notes that these species are very patchy in their distribution and may be intermingled at a scale up to an order of magnitude smaller than a fish's jaws. It is implausible that fish are able to exercise any significant degree of selectivity under these circumstances. Non-selective grazing of the algal turf is much more probable, as indicated by other studies of damselfish and surgeonfish grazing on similar turfs (Montgomery, 1980; Montgomery et al., 1980; Lassuy, 1980; de Ruyter van Steveninck, 1984).

Another possibility may relate to the observation that P. flavicauda took an average of 12% of their total bites feeding on plankton and floating particulate matter, whilst S. fasciatus were never observed using this food source. The nutritive value of plankton is considerably greater than that of algae and these organisms are

rapidly digested (Hyslop, 1980; Lassuy, 1984). Hence, this resource may provide a greater proportion of the food requirements of P. flavicauda than is indicated by feeding rate data alone, reducing the potential for competition for food with S. fasciatus.

There is also another reason why competition for food between these species may be minimal. It has already been mentioned that the lagoon of One Tree Reef becomes ponded on the ebb tide, remaining at a higher level than the surrounding sea. Thus water levels within the lagoon remain relatively constant whilst the lagoon is not connected to the open sea. This results in a well defined splash zone in which there is a dense growth of turf algae. This zone is only accessible to grazers for short periods. Both P. flavicauda and S. fasciatus abandon their territories and home-ranges to feed on this algae when water levels are high enough (although A. fuscus and E. mandibularis do not). During this time feeding is intense and there are very few intra- or interspecific aggressive interactions. Individuals make periodic visits back to their territories between bouts of feeding. Istiblennius edentulus appear to obtain most of their food from this intertidal algae. The availability of this rich food supply could effectively mean that algal resources are not limiting to either P. flavicauda or S. fasciatus.

The assumption that algal food resources are limiting may also be flawed because the rubble habitat appears not to be saturated with P. flavicauda. The population density of this species at the study site was low with the consequence that there were large areas of apparently habitable rubble between most territories. Also, although densities of S. fasciatus were much higher, they were very variable and some areas could almost certainly have supported more. Doherty (1982) found no evidence of density-dependent mortality in populations of juvenile Pomacentrus wardi and P. flavicauda at One Tree Reef, when stocked at high densities on experimental patch reefs. He concluded that competition between fish does not control the density of young fish at this site. What seems more likely is that densities are controlled by the availability of recruits of these species (Williams, 1980; Doherty, 1981, 1983) although this is probably not the case at all sites (Sweatman, 1985). Robertson et al. (1981) have concluded that some populations of a territorial, herbivorous, Caribbean damselfish were not at the carrying capacity of the habitat, and Wellington and Victor (1985) have also found herbivorous damselfish populations limited by recruitment rather than resource availability.

The behaviour of P. flavicauda may seem somewhat paradoxical because if resources are not limiting, as suggested by this study, then why do individuals expend large amounts of energy defending territories against other fish? This is probably because turf algae, the primary food of P. flavicauda, are replaced by coralline algae under conditions of high grazing intensity (Vine, 1974; Littler and Littler, 1985) and so areas must be protected from roving herbivores,

such as parrotfish, in order for turf algal communities to become established and persist. Blennies are probably only tolerated simply because the damselfish are incapable of excluding them (they dart into refuge holes inaccessible to P. flavicauda when attacked). It may be easier for individuals of P. flavicauda to expand the territory to meet food requirements rather than to attempt to exclude S. fasciatus. The feeding activities of blennies appear not to be detrimental to P. flavicauda, although in the long term the presence of blennies may prevent P. flavicauda from attaining maximal growth rates, which may in turn reduce reproductive output. Longer term studies and more powerful tests will be required to determine whether this is so.

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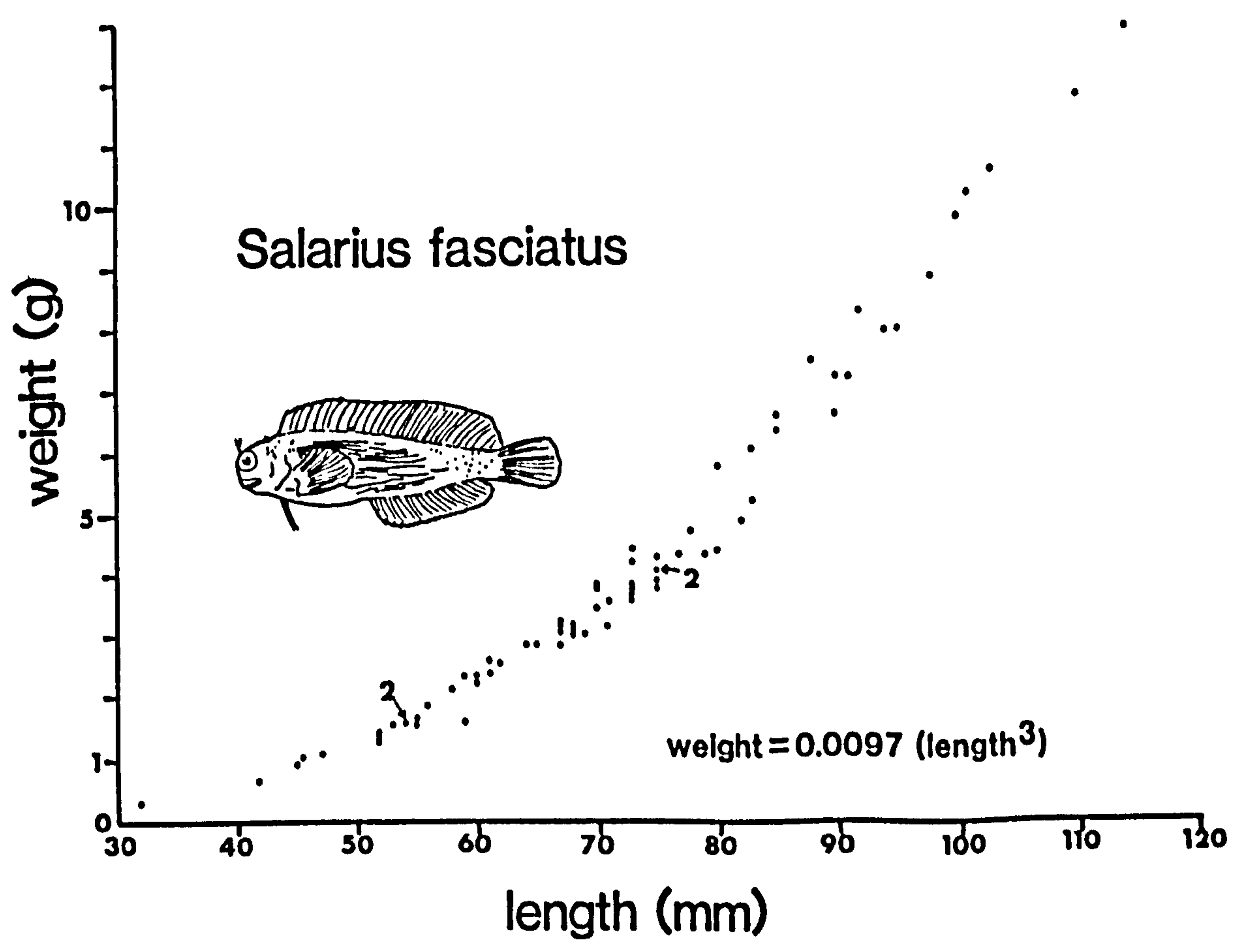
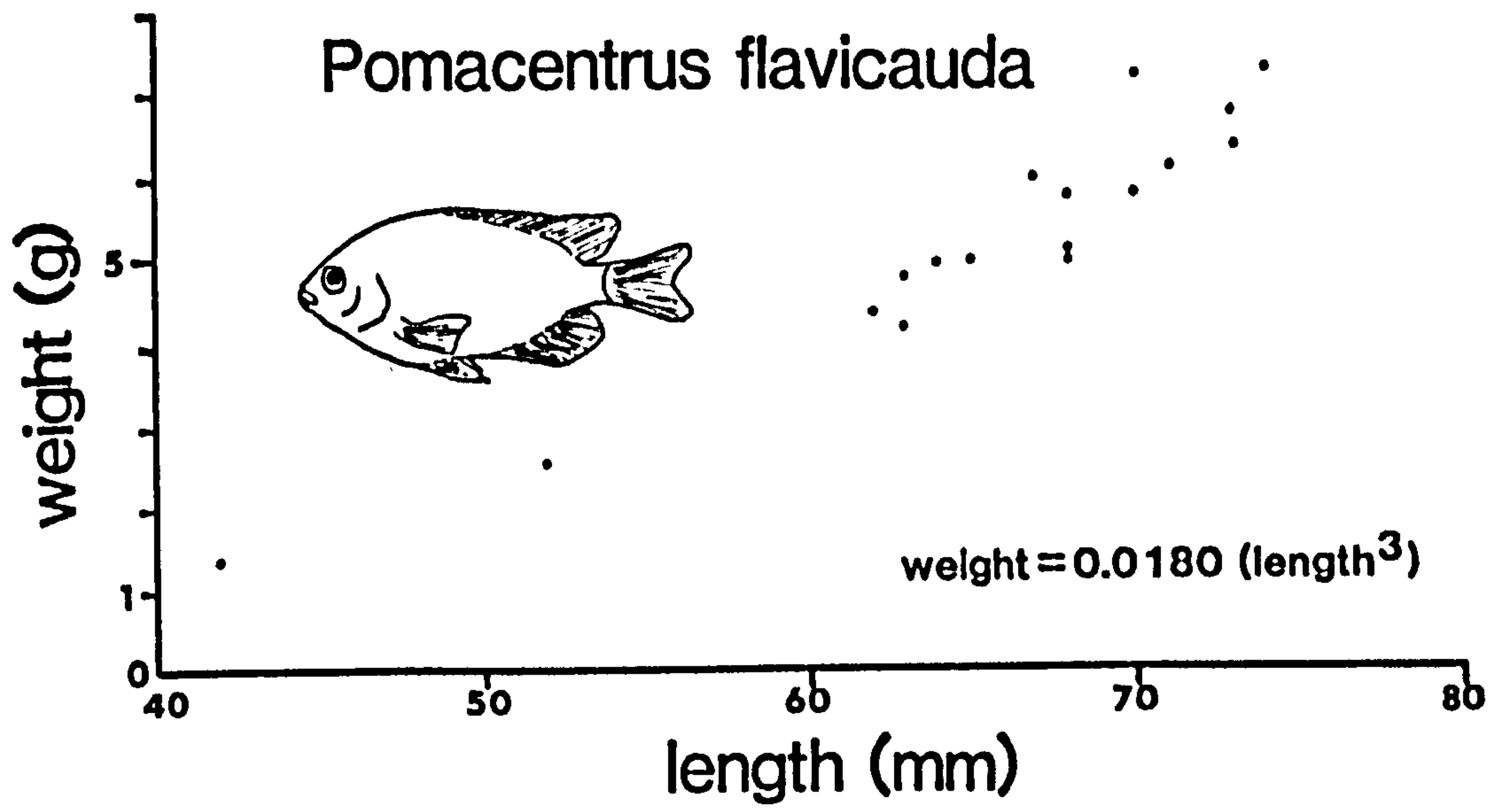
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ADDITIONAL NOTE: Length-weight relationships in P. flavicauda and S. fasciatus. These were calculated according to the equation $W = cL^3$, where W = weight in grammes, L = total length in centimetres, and c is a species-specific constant. Individuals were gutted to eliminate variability due to differences in gut fullness, and blotted dry prior to weighing on a top-pan balance (to nearest 0.1g).

Discussion

DISCUSSION

An important weakness of many previous studies of coral reef fish community structure has been that they have restricted attention to only very limited ranges of scale. For example, many studies in the Caribbean have concentrated on larger scale aspects of the fish communities than similar studies on the Great Barrier Reef and this difference in approach has been at least partially responsible for recent controversy over structuring processes (Sale, 1980; Bohnsack, 1983a; Ogden, 1986). The preceding studies represent a multiscale approach which should allow a fuller understanding of what forces and processes determine and modify the composition of fish communities on coral reefs. However, like any studies they also have limitations, the most important of which is their largely descriptive basis. Experimental studies are, under most circumstances, a more rigorous means by which to test hypotheses (Underwood, 1981). As outlined in the introduction, the logistical basis of work in Saudi Arabia prevented the application of experimental methods in this region. Accepting this limitation though, some useful insights were gained from the research reported in this thesis. These are summarised in the following discussion.

The importance of large scale (geographical) studies has long been realised but has only recently begun to be actively researched (Bohnsack and Talbot, 1980; Anderson et al., 1981; Talbot and Gilbert, 1981; Williams, 1983; Victor, 1984). Several large scale studies of fish communities are now in progress on the Great Barrier Reef but the results of only a few have so far been published (R.H. Bradbury, personal communication). The studies of damselfish, surgeonfish and parrotfish communities along the Saudi Arabian Red Sea coast highlighted some important large scale features of these communities. The composition of communities from different regions of this coast differed markedly. These differences are most pronounced when communities are described only in terms of presence or absence of their component species, although similar patterns emerge from consideration of quantitative data. Differences in the species composition of fish communities over long distances are well known (Ehrlich, 1975; Goldman and Talbot, 1976) but what is important about these studies is that they indicate that regional differences in habitat have a strong influence on this variation. On the Saudi Arabian coast habitat differences appear to have a much greater influence on fish community structure than does latitude-related variation (although latitude-related differences in water temperature may have an indirect effect on fish through possible effects on the coral community, or a direct effect on fish larvae). Preliminary studies on the Great Barrier Reef, a region covering a similar latitudinal range to the Saudi Arabian coast, support these findings. Cross-shelf (longitudinal) variation in fish community structure is

considerably greater than latitudinal variation (Williams, 1983). Differences in habitat on reefs across the continental shelf in the Great Barrier Reef region are very similar to those found between different regions of coast within the Red Sea. Inshore reefs of the Great Barrier Reef are typically shallow, turbid and rather poorly developed, whilst mid-shelf and outer shelf reefs are well developed and have much higher levels of water turbidity (Done, 1982). These studies indicate that at large scales there is a strong deterministic component to coral reef fish community structure.

The regional fauna of the Red Sea and Great Barrier Reef are very different although they do have a proportion of species in common. However, the existence of similar habitat gradients in the two regions would allow an examination of the effects of habitat on fish guild structure. Such a comparison would be very illuminating in that it would indicate whether there exists a further level of determinism in fish community structure: that of trophic structure. The data set presented in this thesis and that of Williams (unpublished data) from the Great Barrier Reef mean that this comparison is now possible.

Smaller scale structure of fish communities, at the within-reef level, has been described in Chapters 3 and 4 of this thesis. It is apparent from Chapter 4 that partitioning of the reef environment at a relatively broad scale is pronounced amongst damselfish in the Red Sea. Other studies indicate that this is a general phenomenon amongst damselfish, and many other families, throughout the tropics (Jones and Chase, 1975; Clarke, 1977; Itzkowitz, 1977; Gladfelter and Gladfelter, 1978; Russ, 1984). Allen (1975) believes that within-reef distributions of damselfish are broader in species-poor areas (such as remote Pacific islands) than in species-rich areas (such as the Great Barrier Reef). It is often true that, within sites, species from species-rich families (like damselfish) generally have more restricted zonations than those from less species-rich families (like surgeonfish or parrotfish) (Hiatt and Strasburg, 1960; Chave and Eckert, 1974; Talbot and Goldman, 1972; Harmelin-Vivien, 1977). However, whether this is significant or not is unknown since no quantitative between-region comparisons of single families have yet been made to verify this observation, despite its obvious significance to niche theory. If distributions of species are broader in species-poor areas compared with species-rich areas then this suggests that niche breadth is compressed by interspecific competition in the species-rich communities (Diamond, 1975).

The study of damselfish vertical zonation patterns in Chapter 3 is typical of many which purport to support theories of coexistence based on resource partitioning arguments (e.g. Smith and Tyler, 1972; Robertson and Lassig, 1980; Waldner and Robertson, 1980). However, like these studies it is descriptive and the findings are open to a number of interpretations. The observed differences between species clearly do contribute to the richness of the fish fauna inhabiting reefs by

enhancing the between-habitat component of diversity. Whether these differences are due to interspecific competition though remains uncertain (Connell, 1980). There is some evidence of resource partitioning in Chapter 3 which is suggestive of interspecific competition (either present or past) between species, that of quantitative differences in the distributions of members of the same guild. That these differences in space use are more pronounced amongst fish strongly associated with the substratum (territorial herbivores) and become less so with decreasing strength of association (omnivores and planktivores), is perhaps the best evidence of interspecific competition that this study can provide. However, these differences were only shown in detail for one site. Additionally, any temporal variations in damselfish zonation, either short-term or long-term, are ignored (although these are unlikely to be large due to the very small home-ranges of most species [Sale, 1978a]). The only satisfactory way of testing whether the observed distribution patterns are the result of competition would be through experiments involving transplantations and removals of species (using fish of all post-settlement life stages since any competitive effect may be restricted to a particular stage).

Chapter 3 also shows that damselfish species differ in their use of space resources at a finer scale: within reef zones. This is important since, until recently, species inhabiting the same zone have often been considered ecologically equivalent (Sale, 1977; Sale, 1978b). The existence of subtle differences in microhabitat use amongst species from the same guild, largely consistent between sites, also lends evidence to resource partitioning based theories of coexistence. These differences are again most apparent amongst the territorial herbivores, the species most closely associated with the substratum. Again though, it is impossible to say without experimentation whether these differences facilitate coexistence or whether they are irrelevant to it.

Chapter 4 differs from the others in this thesis in that, rather than using a species-based approach, it looks at the influence of reef structure on fish community parameters such as species richness and abundance. This is important to the broader questions of what factors allow some habitats to support more species than others and why fish are more abundant in some parts of the reef than in others. Many studies have shown a link between structural complexity of a habitat and the species richness of the resident animal community (MacArthur and MacArthur, 1961; Risk, 1972; Tonn and Magnuson, 1982). This finding has often been interpreted to mean that complex habitats provide more opportunities for resource partitioning between species and hence support more species than simple ones, and also that they provide more opportunities for prey to avoid or escape from predators (enemy-free space [Jeffries and Lawton, 1984]). The study presented here does not test the validity of these interpretations but seeks to find whether such a relationship is demonstrable on Red Sea coral

reefs, and if it does, whether it applies to only part, or most of the fish community. Only a weak relationship was found between structural complexity and species richness and this was not uniform between fish families. It could be argued that this is a result of the limited number of sites studied, or the indirect method of sampling structural complexity (estimation from stereo-photographs), or the fact that water depth was a confounding variable. However, Sale and Douglas (1984) have found a similarly weak relationship in patch reef fish communities using a larger number of sites, at similar depths, and using a direct sampling strategy. Whilst structural complexity does go some way towards understanding how small, strongly site-attached species use the environment, and the inferred (but untested) means by which they coexist, its effect is not spread over the whole fish community. Hence it is insufficient to suggest that tropical reefs support more species-rich fish communities than temperate ones simply because they are more structurally complex, although this probably contributes significantly to the observed differences.

Territorial herbivorous fishes, particularly damselfish, have been at the centre of debate over structuring processes in reef fish communities for some years. Sale developed his lottery hypothesis working on damselfish from this guild on the Great Barrier Reef (Sale, 1974; 1976; 1979) and others have used them to argue that more conventional ecological theory is sufficient to explain fish coexistence on reefs (Robertson and Lassig, 1980; Waldner and Robertson, 1980). However, by restricting attention only to damselfish, these studies failed to consider a phenomenon of much interest to those involved in the study of fish diversity on reefs: that of territory sharing between species with very similar resource requirements, but from different families. These species coexist despite their similarity in use of both space and food resources, and appear to do so through a combination of size differences and behavioural adaptations which prevent exclusion by aggressive interference competition. A mutualistic interaction between damselfish and surgeonfish is suggested but without experimentation cannot be distinguished from a system in which competing species coexist using the same resources (Vance, 1984). Blennies however, are apparently 'food parasites' of damselfish and surgeonfish which species from these latter families are unable to exclude from their territories. This system offers no evidence of coexistence through resource partitioning (between species from different families). Neither does Sale's lottery hypothesis need to be invoked to explain coexistence (although it could be argued that it may operate between species within these families). The interactions between species from different families are facultative (any given species may be present in the absence of the others) and are sufficiently well established over an evolutionary timescale to involve many different suites of species in different regions of the tropics. Territorial herbivores,

whilst abundant on reefs, do not comprise a very large proportion of all reef-inhabiting fish species. Hence, if restricted to these species, this mechanism of coexistence can only go a small way towards explaining the high diversity of coral reef fish communities. However, it is not inconceivable that similar mechanisms exist amongst other groups of territorial species (which have similar resource requirements), where exclusion of one species by another is prevented by the use of refugia accessible to members of only one species.

The data presented in this thesis and information derived from other recent research allow the formulation of a general verbal model of structuring processes in coral reef fish communities. This model is illustrated in the form of a flow diagram (Figure 1) and emphasises the interaction of both deterministic and stochastic processes. The start point is a regional fauna of species which occur over a broad area, such as the western Indian Ocean or the Indo-Australian archipelago. The fauna inhabiting any given area within this region is determined by large scale geophysical and oceanographic processes (which affect patterns of larval distribution and mortality), and by regional habitat types. Stochastic effects during larval dispersal affect the potential recruits which actually arrive at any given reef, and the nature of the reef will govern its suitability as a settlement site for each species. Varying degrees of habitat selection are apparent in different species based on both physical features of the habitat and the composition of the resident fish community. These deterministic effects are overlaid by chance factors coming mainly from the vagaries of larval transport and periodic disturbance of both habitat and resident fish community. Interactions between species at the time of settlement and after this tend to promote determinism in community structure, although it is very unlikely that equilibrium communities, in the conventional sense (stable species composition and densities), will ever become established on coral reefs.

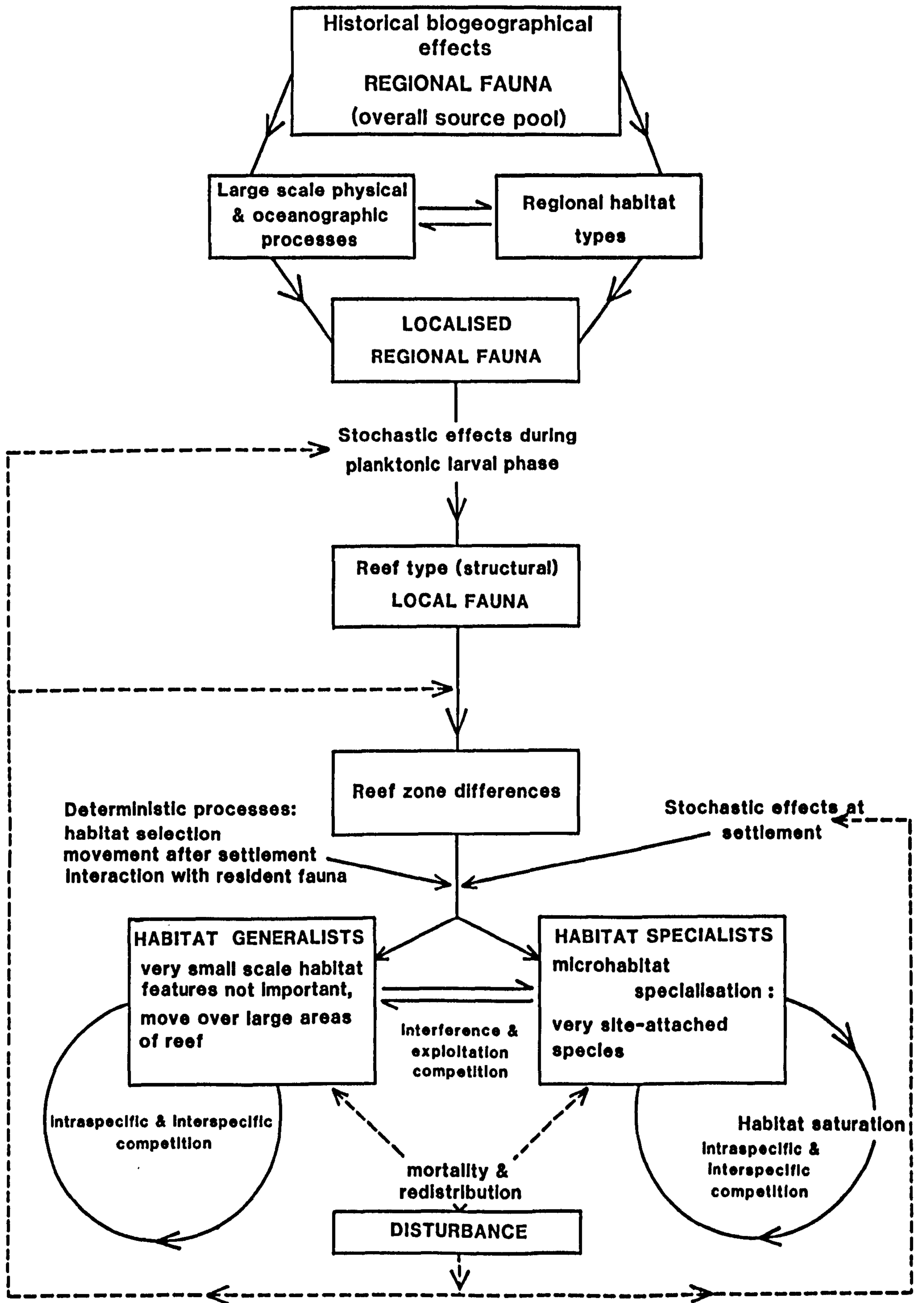


Figure A: General verbal model of structuring processes in coral reef fish communities.

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Appendix 1

Data tables.

Species	HAQL	RAS SUWAYHIL AS SAGHIR	B'IR MARSHAH	AYNUNAH BAY	GORDON'S REEF	TIRAN IS. N.W.	SINAFIR IS. S.W.	SHELSHA IS. S.E.	BARQAN IS. N.	BARQAN IS. W.	YUBA IS. S.W.	30cm N. SHAFM JUBBA	STILA IS. S.E.	SHAFI JUBBA	10cm S. DHUBA	NA'YAN IS. N.E.	MARSA ZUBAIDA	GHUBBET BAL'AKSH	AL WADJ	RAS BARIDI	RABIGH	RAS HATIBA	JEDDAH NCNS	JEDDAH NCSS	AL LITH	RAS MAHSIN	QUNFIDHAH	RAKA	BTAN RAKA & KHOR AMIQ	RAKA	NEAR KHOR AMIQ	NEAR KHOR AMIQ	25cm S. KHOR AMIQ	30cm S. AL BIREK	OPPOSITE QADIMBAL IS.	25cm S. AL QERNA	RAS AL ABYADH		
<i>Chromis dimidiata</i>	55	70	108	0	128	120	94	69	41	81	111	156	36	55	44	385	0	152	37	226	292	301	501	421	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>C. ternatensis</i>	0	0	0	0	0	0	0	23	1	3	25	82	0	0	15	58	25	0	0	9	162	351	5	2	0	0	0	6	81	6	181	148	195	0	1	11	0	0	
<i>C. caerulea</i>	0	20	3	7	0	6	0	197	134	20	0	40	20	0	3	59	81	0	10	21	23	670	22	0	0	0	93	69	93	1043	509	248	0	256	514	76	0		
<i>Neomimacentrus miryae</i>	0	0	0	979	0	0	0	25	1	0	5	12	0	0	0	0	24	0	0	0	0	39	2	0	0	0	165	394	942	600	265	1135	125	350	310	238	6		
<i>N. xanthurus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	123	38	203	37		
<i>N. cyanomos</i>	0	0	0	0	7	0	0	101	0	0	7	47	0	0	0	4	43	0	0	2	8	53	118	39	0	136	56	171	121	50	67	158	61	23	203	37			
<i>Abudefduf sexfasciatus</i>	1	13	4	0	0	0	0	0	0	0	0	106	0	31	0	13	2	0	1	0	0	0	1	10	1	0	0	0	0	0	0	0	0	50	4	0	12		
<i>A. saxatilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>A. sordidus</i>	2	0	8	0	0	0	2	43	1	0	18	0	0	0	45	19	83	0	0	2	0	9	0	1	0	0	0	3	0	0	0	0	0	0	0	0	0		
<i>Amblyglyphidodon leucogaster</i>	0	0	0	48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	127	0	14	15	14	16	24	11	94	0	1	1		
<i>A. flavilatus</i>	39	28	50	0	69	49	15	42	50	55	6	94	3	14	111	77	95	71	16	50	20	29	25	12	2	6	0	15	8	15	12	9	27	0	11	20	10		
<i>Pomacentrus sulfireus</i>	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	5	0	5	2	5	5	5	28	0	22	15	5		
<i>P. agilis</i>	0	0	0	7	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	110	183	265	205	132	205	138	215	143	98	55	113	51	
<i>P. trilineatus</i>	1	4	0	0	22	0	3	0	17	12	8	46	8	0	0	0	3	18	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Plectrogllyphidodon leucozonus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chrysiptera unimaculata</i>	7	9	1	0	0	0	0	0	5	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	
<i>Plectrogllyphidodon lacrymatus</i>	61	9	3	26	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Pomacentrus trichourus</i>	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Muscylus armatus</i>	0	0	4	2	0	1	0	0	0	0	0	1	0	0	0	1	2	2	0	0	1	1	0	0	0	2	5	1	4	0	8	4	4	0	2	0	2		
<i>Parabllyphidodon melas</i>	2	3	3	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	3	0	0	3	0	0	2	0	0	0	1	0	
<i>Amphiprion bicinctus</i>	0	0	0	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Pristotis cyanostigma</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Muscylus trimaculatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	13	16	92	
<i>D. marginatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Pomacentrus albicaudatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	3	
<i>P. leptus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

NUMBERS OF DANSELFISH COUNTED ON 100 x 5m TRANSECTS LAID AT 1.5m DEEP AT THE REEF-EDGE AT SITES ON THE SAUDI ARABIAN COAST.

	<i>Acanthurus</i> <i>scha</i>	<i>A. nigricans</i>	<i>A. nigrofuscus</i>	<i>Naso unicornis</i>	<i>N. lituratus</i>	<i>N. brevirostris</i>	<i>N. hexacanthus</i>	<i>Zebrasoma veliferum</i>	<i>Z. xanthurum</i>	<i>Ctenochaetus striatus</i>
HAQL	0	0	1	0	0	0	0	0	1	1
RAS SUWAYHIL AS SAGHIR	0	0	1	0	0	0	0	0	1	1
B'IR MARSHAH	0	0	1	0	0	0	0	0	1	1
AYNUNAH BAY	0	0	0	0	0	0	0	1	0	0
TIRAN IS. W.	1	0	1	1	1	0	0	1	1	1
GORDON'S REEF	0	0	1	0	0	0	0	0	0	0
SINAFIR IS.	1	0	1	0	0	0	0	1	1	1
SIUSHA IS.	1	0	1	0	1	0	0	1	0	1
BARQAN IS. N.	0	0	1	0	1	0	0	1	1	1
BARQAN IS. W.	1	0	1	0	1	0	0	0	0	1
YUBA IS.	1	0	1	0	1	0	0	1	0	1
30km N. SIARM JUBBA	1	0	1	0	0	0	0	0	1	1
SILA IS.	1	0	1	0	0	0	0	0	0	1
SIARM JUNBA	1	0	1	1	0	0	0	1	0	1
PATCH REEF S.W. SIARM JUNBA	1	1	1	1	1	1	1	1	1	0
10km S. DIRUBA	1	0	1	1	1	0	0	1	0	1
NA'MAN IS. N.E.	0	0	1	0	0	0	0	1	1	1
MARSA ZUBAIDA	1	0	0	1	0	1	0	1	0	1
GHUBBET BAL'AKSH	1	1	1	0	0	0	0	1	1	1
AL WADJ	1	0	1	0	1	0	1	1	1	1
RAS BARIDI	1	1	1	1	1	0	0	1	1	1
RABIGH	1	0	1	1	1	0	0	1	1	1
JEDDAH NCNS	1	0	1	1	1	1	1	1	1	1
JEDDAH NCSS	1	0	1	1	1	0	1	1	1	1
SOUTHERN CORNICHE	1	0	1	1	1	0	0	1	1	1
SUU'AIBA	1	1	1	1	1	0	1	1	1	1
AL LITH	0	1	0	0	0	0	0	1	0	0
RAS MAHASIN	1	1	0	1	0	0	0	1	0	1
QUNFIDIAH	1	1	0	0	0	0	0	1	0	1
BTWN RAKA & KIOR AMIQ	1	1	0	0	0	0	0	1	0	1
RAKA	1	1	0	0	0	0	0	1	0	1
NEAR KIOR AMIQ	1	1	0	0	0	0	0	1	0	1
NEAR KIOR AMIQ	1	1	0	0	0	0	0	1	0	1
25km S. KIOR AMIQ	1	1	0	0	0	0	0	1	0	1
3km S. AL BIRK	0	1	0	0	0	0	0	1	0	0
8km S. AL BIRK	1	1	0	0	0	0	0	1	0	1
10km S. AL BIRK	0	1	0	0	0	0	0	1	0	0
1km N. AL QUMA	0	1	0	0	0	0	0	1	0	0
AL QUMA	0	1	0	0	0	0	0	1	0	1
AL QUMA	1	1	0	0	0	0	0	1	0	1
OPPOSITE QADIMMAL IS.	1	1	0	0	0	0	0	1	0	1
25km S. AL QUMA	1	1	0	0	0	0	0	1	0	1
RAS AL ABYADH	1	1	0	0	0	0	0	1	0	1
BAB AL ABYADH	0	1	0	0	0	0	0	0	0	0
13A11	0	1	0	0	0	0	0	0	0	0
13G01	0	1	0	0	0	0	0	0	0	0
13H04	0	1	0	0	0	0	0	0	0	0

SURGFISH SPECIES PRESENCE/ABSENCE ALONG THE SAUDI ARABIAN RED SEA COAST.

	<i>Acanthurus sobal</i>	<i>Ctenochaetus striatus</i>	<i>Acanthurus nigrofuscus</i>	<i>Naso unicornis</i>	<i>N. lituratus</i>	<i>N. hexacanthus</i>	<i>Zebrasoma veliferum</i>	<i>Z. xanthurum</i>	<i>Acanthurus nigricans</i>
HIAQL	0	3	30	0	0	0	0	4	0
RAS SUWAYHIL AS SAGHIR	0	9	84	0	0	0	0	9	0
B'IR MARSHAH	0	7	51	0	0	0	0	9	0
AYNUNAH BAY	0	0	0	0	0	0	3	0	0
GORDON'S REEF	0	0	12	0	0	0	0	0	0
TIRAN IS. W.	15	7	14	2	10	0	24	3	0
SINAFIR IS.	1	4	120	0	0	0	7	3	0
SHUSIA IS.	0	15	9	0	5	0	6	0	0
BARQAN IS. N.	0	17	2	0	3	0	8	2	0
BARQAN IS. W.	6	8	20	0	1	0	0	0	0
YUBA IS.	9	11	21	0	1	0	2	0	0
30km N. SIARM JUBBA	21	2	4	0	0	0	0	1	0
SILA IS.	27	14	15	0	0	0	0	0	0
SIARM JUBBA	29	10	65	0	0	0	6	0	0
10km N. DIUBA	4	7	29	1	2	0	5	0	0
NA'MAN IS.	0	4	2	0	0	0	3	2	0
MARSA ZUBAIDA	58	12	0	31	0	0	3	0	0
GHUBBET BAL'AKSH	69	2	16	0	0	0	8	0	0
AL WADJ	70	27	26	0	2	0	9	0	0
RAS BARIDI	41	114	113	0	1	0	14	2	0
RABIGH	40	32	10	4	1	0	1	0	0
JEDDAH NCNS	24	31	4	12	12	0	2	0	0
JEDDAH NCSS	22	27	19	1	10	9	1	0	0
SOUTHERN CORNICHE	32	109	29	0	6	0	2	2	0
AL LITH	0	0	0	0	0	0	3	0	3
RAS MAHASIN	5	3	0	0	0	0	10	0	3
QUNFIDIAH	16	7	0	0	0	0	6	0	6
BTWN RAKA & KIQR AMIQ	14	0	0	0	0	0	0	0	1
RAKA	26	42	0	0	0	0	4	0	1
NEAR KIQR AMIQ	12	4	0	0	0	0	32	0	1
NEAR KIQR AMIQ	43	3	0	0	0	0	0	0	3
25km S. KIQR AMIQ	37	32	0	0	0	0	7	0	11
3km S. AL BIRK	0	0	0	0	0	0	13	0	2
OPPOSITE QADIMBAL IS.	25	0	0	0	0	0	2	0	7
25km S. AL QUIMA	31	3	0	0	0	0	2	0	0
RAS AL ABYADH	12	3	0	0	0	0	1	0	7

SURGEONFISH ABUNDANCE FROM COUNTS ALONG A 100 x 5m TRANSECT LAID AT 1.5m DEEP AT THE REEF-EDGE AT SITES ALONG THE SAUDI ARABIAN RED SEA COAST.

	Scarus sordidus	S. ferrugineus	S. frenatus	S. ghobban	S. gibbus	S. psittacus	S. niger	S. fuscopurpureus	Hipposcarus harid	Calotomus viridescens	Cetoscarus bicolor	Bolbometopon muricatum
HAQL	1	1	1	0	1	1	1	1	1	1	0	0
RAS SUWAYHIL AS SAGHIR	1	1	1	0	1	0	1	0	0	0	0	0
D'IR MAISHAH	1	1	1	0	0	1	1	0	0	0	0	0
AYNUNAH BAY	0	0	0	1	0	0	0	0	0	0	0	0
TIRAN W.	1	1	1	0	1	1	1	1	1	0	1	0
GORDON'S REEF	1	1	1	0	0	1	1	1	0	0	0	0
SINAFIR S.W.	1	1	1	1	1	1	1	0	1	0	1	0
SIUSIA IS.	1	1	1	1	1	0	1	1	1	0	1	0
BARQAN IS.	1	1	1	0	0	0	1	0	1	0	1	0
YUBA IS.	1	0	1	0	1	1	1	0	0	0	0	0
30km N. SHARM JUBBA	1	1	1	0	0	1	1	1	1	0	1	0
SILA IS.	1	0	1	0	0	0	1	0	1	0	1	0
SHARM JUBBA	1	1	1	0	1	1	0	0	1	0	1	0
NA'MAN IS. N.E.	1	1	1	0	0	0	1	0	1	0	0	0
NA'MAN IS.	0	0	1	1	1	1	0	0	1	0	0	0
MARSA ZUMAYDA	1	1	1	1	1	0	1	1	1	0	1	0
GIUBBET BAL'AKSH	1	1	1	0	1	0	1	1	1	0	1	0
AL WADJ	1	0	1	1	1	1	1	1	1	0	1	0
RAS BARIDI	1	1	1	0	1	1	1	0	1	0	1	0
RABIGH	1	1	1	1	1	1	1	1	1	0	1	0
RAS HATIBA	1	1	1	0	1	1	1	0	1	0	1	0
JEDDAH NCNS	1	1	1	0	1	1	1	1	1	1	1	1
JEDDAH NCSS	1	1	1	1	1	1	1	1	1	0	1	1
SOUTHERN CORNICHE	1	1	1	0	1	1	1	0	1	0	1	1
SHU'ATHA	1	1	1	1	1	1	1	1	1	1	1	1
AL LITH	1	0	0	0	0	0	0	0	1	0	0	0
RAS MAHASIN	1	1	0	1	1	0	1	0	1	0	0	1
QUNFIDIAH	1	1	0	1	0	0	1	0	1	0	0	0
BTWN RAKA & KHOR AMIQ	1	1	0	1	0	1	1	0	1	0	0	0
RAKA	1	1	0	0	0	1	1	0	1	0	0	0
NEAR KHOR AMIQ	1	1	0	1	0	1	1	0	1	0	0	0
NEAR KHOR AMIQ	1	1	0	1	0	1	1	0	0	0	0	0
25km S. KHOR AMIQ	1	1	1	1	0	1	1	1	1	0	0	0
3km S. AL BIRK	1	1	0	0	0	1	0	0	1	0	0	0
8km N. AL BIRK	1	1	0	1	1	1	1	0	1	0	1	0
10km S. AL BIRK	0	0	0	0	0	1	0	0	0	0	0	0
1km N. AL QUJMA	1	1	0	0	0	1	0	0	1	0	0	0
AL QUJMA	1	1	0	0	0	1	1	0	1	0	0	0
AL QUJMA	1	1	0	1	0	0	0	0	1	0	0	0
OPPOSITE QADIMBAL IS.	1	1	0	1	0	1	0	0	0	0	0	0
25km S. AL QUJMA	1	1	0	0	0	1	1	0	1	0	0	0
RAS AL ABYADH	1	1	0	1	0	0	1	0	1	0	0	0
BAB AL ABYADH	0	1	0	0	0	0	0	0	0	0	0	0
13G01	0	1	0	1	0	0	0	0	0	0	0	0
13H04	0	0	0	1	0	0	0	0	0	0	0	0

PARROTFISH SPECIES PRESENCE/ABSENCE AT SITTS ON THE SAUDI ARABIAN RED SEA COAST.

	Scarus sordidus	S. ferrugineus	S. frenatus	S. globban	S. gibbus	S. psittacus	S. niger	S. fuscopurpureus	Hipposcarus harid	Cetoscarus bicolor
HIAQL	9	0	1	0	0	1	5	0	0	0
RAS SUWAYHIL AS SAGHIR	12	7	4	0	1	0	10	0	0	0
B'IR MARSHAH	3	2	6	0	0	3	8	0	0	0
AYNUNAH BAY	0	0	0	1	0	0	0	0	0	0
GORDON'S REEF	4	2	1	0	0	0	4	3	0	0
TIRAN IS. W.	5	0	4	0	1	0	4	10	0	1
SINAFIR IS.	31	4	7	7	1	1	4	0	22	2
SIUSHA IS.	5	4	2	1	1	0	2	2	7	1
BARQAN IS. N.	9	8	5	0	0	0	6	0	1	3
BARQAN IS. W.	3	1	5	0	0	1	4	0	0	0
YUBA IS.	2	0	5	0	1	1	1	0	0	0
30km N. SHARM JUBBA	1	1	1	0	0	2	2	3	1	1
SILA IS.	3	0	3	0	0	0	1	0	10	1
SHARM JUBBA	2	2	4	0	2	1	0	0	6	4
10km S. DIUBA	14	0	1	1	1	2	4	0	18	1
NA'MAN IS.	19	2	1	0	0	0	4	0	7	0
MARSA ZUBAIDA	19	3	4	15	2	0	2	3	8	3
GHUBBET BAL'AKSH	2	2	10	0	1	0	11	1	3	1
AL WADJ	2	0	1	0	1	0	0	0	2	2
RAS BARIDI	6	1	6	0	0	0	8	0	2	0
RABIGH	3	0	5	0	0	1	1	1	3	1
RAS HATIBA	7	3	0	0	0	1	3	0	0	0
JEDDAH NCNS	5	4	1	0	0	0	1	0	18	0
JEDDAH NCSS	7	7	0	0	0	1	3	0	5	1
SOUTHERN CORNICIE	12	2	2	0	1	0	4	0	1	0
AL LITH	4	0	0	0	0	0	0	0	0	0
RAS MAJASIN	6	25	0	4	0	0	3	0	21	0
QUNFIDIAH	4	13	0	3	0	0	1	0	1	0
BTWN RAKA & KHOR AMIQ	4	2	0	1	0	0	1	0	0	0
RAKA	15	18	0	0	0	0	1	0	0	0
NEAR KHOR AMIQ	8	27	0	6	0	1	9	0	4	0
NEAR KHOR AMIQ	2	26	0	0	0	0	4	0	0	0
25km S. KHOR AMIQ	19	18	1	1	0	30	10	0	0	0
3km S. AL BIRK	1	6	0	0	0	2	0	0	2	0
OPPOSITE QADIMBAL IS.	10	21	0	0	0	0	0	0	0	0
25km S. AL QUJMA	8	7	0	0	0	0	0	0	0	0
RAS AL ABYADI	11	17	0	1	0	0	1	0	1	0

PARROTFISH ABUNDANCE ON 100 x 5m TRANSECTS LAID AT THE REEF-EDGE AT SITES ALONG THE SAUDI ARABIAN RED SEA COAST.

Appendix 2

The study of fish territoriality: a review of methods.

ABSTRACT

Many methods have been used to study territoriality in fish, both observational and experimental. A typical methodology for plotting territories involves first the marking out and mapping of the study area. Maps are usually sketched and must be drawn to scale. For long-term studies the site could be photographed and a photomosaic prepared. This can be sealed between perspex sheets for use underwater. Subjects can be identified individually by variations in colour pattern, scars, minor deformities, size, sex and location, or can be tagged. Delineation of territories may be achieved by several methods: (1) locations of aggressive interactions between resident(s) and intruders are marked on the site map, (2) movements of resident(s) are followed continuously on the map, or (3) position of the subject(s) is marked on the map at intervals which may be timed or defined in other ways, such as each time the subject changes direction or feeds. Boundaries can sometimes be inferred from differences between the substratum inside and outside territories. The major problem faced when plotting territories by following the movements of fish arises from extra-territorial movements. Types of extra-territorial movements are described and cues by which they may be recognised outlined. The measurement of time-budgets of territory holders provides information with which hypotheses about the nature and economics of territoriality can be verified. The intensity of aggressive interactions between conspecifics and between heterospecifics has considerable behavioural and ecological importance and can be quantified through observations of displays and movements of the subject. Hypotheses about the functions of territoriality formulated from observational evidence can be tested through experimentation. Experimental approaches are of three main types: (1) introduction to territory holders of novel fish either live (enclosed in jars), dead (encased in resin), or modelled from various materials, (2) manipulation of resources within territories (e.g. food supplementation or removal), and (3) removal of individuals from, or addition of them to, areas of established territories. Various methodological and interpretational problems are identified and

discussed.

INTRODUCTION

Territoriality is a widespread phenomenon throughout the animal kingdom and has been defined in many ways (Kaufman 1983). Territories have been defined most simply as defended areas (Noble 1939) but this definition is rather restrictive. Kaufman (1983) has discussed in detail the various definitions of territoriality and himself opts for one which is more inclusive. This states that a territory holder should have priority of access to resources in some area (which is fixed) and that this dominance must be achieved through social interaction. However, he does not believe overt aggression in defence of the area is a prerequisite for territoriality. Territories may be maintained through mutual avoidance. Trespass onto the territory by other individuals is also permitted in his definition. This broader view of territoriality is the one accepted in this paper.

Territoriality in fishes is very common and is generally considered a multifunctional phenomenon (Hixon 1981). In contrast to the predominantly intraspecifically defended territories of terrestrial vertebrates, many fish defend territories against a range of species (e.g. Low 1971; Myrberg and Thresher 1974; Robertson and Polunin 1981). Territoriality in terrestrial vertebrates is also usually transient, lasting through the breeding season, whilst fish frequently hold permanent territories (Sale 1978a). In studies of marine fish, most effort has been directed at species of the family Pomacentridae (damselfish). These fish seem to hold territories primarily as feeding areas but territories also usually contain shelter holes and, in the case of males, nesting sites (Sale 1978a). However, food need not always be the most important resource defended. Moran and Sale (1977) found that in the damselfish Parma microlepis, defence was primarily against space related competitors rather than food related ones. They found a strong association between the population density of this species and the availability of shelter. The studies of Low (1971) and Hixon (1981) have also emphasised the importance of shelter.

Whilst many species of fish hold individual territories (e.g. Sale 1974; Nursall 1977), more complex systems of territoriality are

known. For example, pair territoriality (e.g. Robertson 1979; Pressley 1981; Ormond 1972), group territoriality (Sale 1978a), lek territories (Loiselle and Barlow 1978; Warner and Hoffman 1980), and nested territories (Kuwamura 1984). Many different methods have been used to map the territories of fish and it is the aim of this review to outline the most commonly used approaches and discuss their limitations. Although I am concerned predominantly with the study of territoriality, the methods described involving the mapping of fish movements may be applied to investigation of any form of space-related behaviour in fish. In addition, experimental approaches to studies of territoriality will be described and discussed.

THE STUDY AREA

The preliminary stage in any investigation of territoriality involves selection of the study site or sites. In doing this the aims of the research should be of primary importance but practicalities should also be considered. The accessibility of the site, depth, tidal regimen, currents, turbidity, exposure and human disturbance all influence the amount of time which may be spent on direct observations and the quality of these.

Having selected the study site(s) at which the investigation is to be carried out, the area must first be marked out. Sites are usually marked using buoys to enable them to be easily relocated on subsequent visits. The area in which observations are to be focussed should also be clearly defined underwater. Sometimes local topography suffices, for example a small lagoonal patch reef needs no further marking for its boundaries to be clearly distinguished. The 'home' anemone of anemonefish is likewise clearly defined (Ross 1978; Moyer 1980). Gronell (1980) in her study of the damselfish Stegastes variabilis (= Eupomacentrus variabilis) was able to locate her site by its proximity to a submarine electric cable. Most sites are less clearly defined topographically and need to be marked to simplify position finding when mapping territories. For large areas the simplest method of doing this is to divide the area into a grid. This has been done using polypropylene ropes (Clarke 1970; Sale 1978b; Roberts in press), wires (Low 1971), coded plastic tapes tied to the substratum (Larson 1980), or small numbered floats anchored by

concrete blocks (Hixon 1981). If the sites are small and well spaced out, such as isolated coral heads, there is no advantage in marking out the area in this way. Such sites are best marked using tags. Pressley (1981) labelled some of his sites with numbered stainless steel tags, whilst Itzkowitz (1977) used plastic tags with numbers encoded by drill holes and nailed them into the substratum. Clarke (1970) initially marked nest sites, shelter holes and other reference points with labelled bricks in his study of the damselfish Hypsypops rubicunda. Similarly, Kohda (1981) marked positions where study fish appeared to have territories by using numbered balls placed on the bottom.

Prior to plotting territories of subject fish, a map should normally be made of the study site. The simplest method of mapping the site is by sketching it in pencil on a roughened perspex board. The map should be drawn to scale and need not record every minor detail of the substratum. The most prominent features of the area should be noted and their spatial relationships carefully established through measurement. The detail which must be recorded on the map will depend on the scale of movements of the study species. A more detailed map is required to plot territories of fish with small ranges of movement (e.g. blennies) than with large ranges of movement (e.g. parrotfish). If a grid has been set up to mark the area, the boundaries and intersections of this should be marked. In relatively featureless areas, such as sand bottoms, the map will largely consist of such artificial reference points. For more detailed or long-term studies the area may be photographed and a photomosaic constructed (Sale 1978b; Weinberg 1981). Sketch maps can be redrawn onto perspex in waterproof pen for short-term studies, or for studies of greater duration, photographs or drawings can be sealed between sheets of perspex (Freeman and Alevizon 1983) or maps can be etched onto perspex (Jones 1981).

IDENTIFYING THE SUBJECTS

Subject fish can be identified with or without tagging. In many studies individuals have been recognised by variations in colouration (Michel et al. 1983; Jones 1984), differences in body size (Kuwamura 1984), minor deformities such as scars (Low 1971; Alevizon and

Landmeier 1984), sex (Norman and Jones 1984) and location (Nursall 1974; Thresher and Moyer 1983). Usually some combination of these is used allowing individual recognition of most fish in the study area. Some features are useful only over short periods such as scars, body size and often sex, whilst variation in colour pattern, deformities and location may remain useful over longer periods.

For studies involving large numbers of fish it is often better to mark some or all individuals. This can be achieved through tagging or fin-clipping. Fin-clipping has been successfully used in several studies (e.g. Sale 1971; Warner and Hoffman 1980) but has the disadvantage that removed tissue is quite rapidly regenerated (the pelvic fins are often regenerated more slowly than other fins). Tags have been more widely used. Different types of tag have different useful lifespans. Popper and Fishelson (1973) used coloured plastic tags sewn into the dorsal musculature anterior to the dorsal fin and were still able to distinguish tagged fish eight months later. Moyer (1980) marked anemonefish with coloured beads sewn into the caudal peduncle but found that these were usually 'cleaned' off within three weeks by the cleaner fish Labroides dimidiatus. Hixon (1981) used colour-coded anchor tags sewn into the base of the dorsal fin and found that most of these became overgrown with algae after a few months. Others have used unique combinations of coloured beads sewn into the base of the dorsal fin or into the dorsal musculature (Nursall 1977; Pressley 1981; Yanagisawa 1982).

Thresher and Gronell (1978) developed a more durable form of tag involving subcutaneous injection of coloured acrylic paint into the fish. Individuals can be tagged uniquely with different colour combinations and the authors claim that the method alleviates problems of tagged fish behaving differently or being more susceptible to predation as a result of tagging. They were still able to distinguish tagged fish after a period of ten months. However, in some regions, such as the Great Barrier Reef, this form of tagging leads to high levels of mortality from fungal infections (A.M. Gronell, personal communication). Subcutaneous injection of dyes used in tattooing has proven to be less damaging and has reduced tagging mortality to acceptable levels on the Great Barrier Reef whilst still providing a durable tag (D.J. Ferrell, personal communication).

The trauma to fish resulting from the tagging process must be

minimised. It is also very important that fish are returned to the site of capture. Wilson (1982) describes a method of tagging fish underwater which eliminates trauma due to removal of fish from the water. Capture is by underwater fishing with a hook and line, a technique successfully used by Yanagisawa (1982) and Emery (1973). Others have used set nets (Popper and Fishelson 1973; Clarke 1970), traps (Hixon 1981), hand nets (Larson 1980) and anaesthetics (Pressley 1981) to capture fish for tagging.

Before beginning to plot territories or study behaviour it is important to assess the extent to which tagging has altered the behaviour of the subjects. Larson (1980) found that fish were shy of divers for approximately a week after tagging. Whenever possible, it is better to identify fish without tagging. However, for longer term studies or studies involving large numbers of fish tagging is often essential.

PLOTTING TERRITORIES

The distance from which fish may be observed by a diver without apparently affecting their behaviour must be determined before plotting territories (Reese 1978). This 'discrete distance' varies between species. For example, butterflyfish are best observed from distances of 3-10m (Ehrlich et al. 1977) whilst many damselfish will ignore divers positioned as close as 1m away (Ebersole 1980). At the same time, small fish must be approached more closely than large ones in order to accurately observe their behaviour. With repeated visits to a site, residents may become habituated to the presence of an observer and allow a closer approach (Yanagisawa 1982). Normally, an observer using a snorkel can approach closer than one using SCUBA as the bubbles and noise from the latter may be disturbing. Closed-circuit, rebreather apparatus alleviates this problem (Losey 1978).

There are many approaches to mapping territories. The territory as a defended area (sensu Noble 1939) is frequently plotted by marking on a map of the area the positions of aggressive interactions between the holder and intruders (Ross 1978; Hixon 1981). The locations of aggressive interactions have been defined in two ways. They are either marked as the position of an intruder when it elicits an aggressive

response from the resident, or during chases as the endpoint of the chase (Hixon, personal communication). The latter method is unsuitable for mapping the boundaries of contiguous territories. When territories are contiguous chases may become extra-territorial (Clarke 1970; Nursall 1974) and the former method should be used. The area of non-contiguous territories is calculated as the area enclosed by lines joining the outermost locations of aggressive encounters such that the resulting polygon has no concavities: the convex polygon method (Odum and Kuenzler 1955). The boundaries of contiguous territories are usually clearly defined and concavities are allowable.

In many cases it is not possible to map boundaries by the positions of aggressive encounters since the frequency of overt aggression is too low (Fricke 1980; Gronell 1980; Pressley 1981). Fricke (1980), working on the angelfish Pomacanthus imperator, found that instances of aggression between neighbouring territory holders were very infrequent but could easily be provoked by chasing one fish into another's territory. The absence of overt aggression in defence of the territory does not necessarily mean that individuals are not holding territories. Areas of exclusive use may be maintained through mutual avoidance (Kaufman 1983). Thresher (1979), using an experimental technique, found that the damselfish Stegastes planifrons (= Eupomacentrus planifrons) recognised individuals from neighbouring territories, responding to them with lower levels of aggression than to unfamiliar fish from more distant territories. Reese (1975) tentatively concluded that the low levels of aggression which he observed between neighbouring butterflyfish were explainable on the basis of individual recognition, social relationships being occasionally reinforced by bouts of agonistic behaviour.

When levels of agonistic behaviour are low it is more sensible to map the movements of the subject, it being assumed that these lie within the defended area (technically this is a plot of the home range). For slow moving species it may be possible to follow the movements of the subject continuously on a map of the area (Kuwamura 1984). More information may be added to such a plot by marking the location of a fish at regular intervals, say at the end of each minute of observation (Jones 1984). Additionally, Ormond (1972) marked the locations at which the subject came close to neighbouring territory holders, noting that this often indicates that the territory boundary

lies between these individuals. With faster moving species continuous following of location is not practicable. Here, positions of fish are best marked at intervals. These intervals may be timed, for example Roberts (in press) marked the position of the subject every ten seconds throughout the observation period. However, the intervals at which recordings are made can be defined in other ways. Sale (1974) marked the positions at which fish changed direction and returned to the centre of the territory. Larson (1980) formalised this approach noting positions where fish changed direction by 90° or more. The species in Larson's study (rockfish) were rather sedentary and spent much time resting on the bottom. The positions at which fish rested were also noted. Robertson and Polunin (1981) studied herbivorous fish which feed on algae attached to the substratum and delineated territories by marking the positions of feeding bites. Others have more loosely defined the points at which the position of the subject is marked as simply locations visited and vacated as the fish moved about its territory (Nursall 1977). In practice, it is best to combine the mapping of movements of the subject with the plotting of locations of agonistic interactions if these occur.

The fixing of the locations of the points marked is usually achieved by determining the spatial relationship between the subject and features of the substratum, natural or artificial, which have been mapped. Some workers have marked positions physically using small, coloured weights and subsequently recorded their locations at the end of the observation period (Nursall 1974, 1977; Reese 1978; Hixon 1981). This method is not recommended since the behaviour of fish may be affected by the presence of such novel objects, either avoiding them or being attracted to them (personal observations). Additionally, in order to place the markers the subject must be followed around and this is likely to disturb it.

The length of observation period necessary to define the territory of a fish will vary depending on its activity and the size of the territory. Ebersole (1980) notes that an adequate map could be made of the territory of the damselfish Stegastes leucosticus (= Eupomacentrus leucosticus) in twenty minutes. Robertson and Polunin (1981) studying surgeonfish and damselfish used observation periods of between ten and thirty minutes whilst Freeman and Alevizon (1983) used periods of 120-240 minutes (divided into thirty minute periods) to map

territories of fairy basslets. Odum and Kuenzler (1955) devised an objective method for determination of the minimum duration of observations required to map a territory. They constructed a graph of apparent territory size versus length of observation period and defined the minimum mapping period as the time after which each unit increase in the duration of observations resulted in only a one percent increase in the perceived territory size. Norman and Jones (1984), mapping territories of the damselfish Parma victoriae, used a modified form of this method selecting the period after which, on average, continued observations resulted in only a five percent increase in the perceived size of the territory. Figure 1 shows an example of a time-area plot for an individual of the damselfish Pomacentrus flavicauda. The wide availability of inexpensive, underwater digital watches possessing a stopwatch function has considerably simplified the problem of timing in studies of fish territoriality.

For some species which have very large territories or which are rather sedentary, a map of the territory may have to be built up over many periods of observation at a site. Fricke (1980) constructed territory maps for Pomacanthus imperator from independent sightings of individuals over a period of three months. Larson (1980) surveyed areas for the positions of rockfish rather than focussing on particular individuals, constructing a map of territories from observations made over a period of a year. If using this approach, territory areas should be calculated using the convex polygon method (Odum and Kuenzler 1955). This procedure of mapping territories will probably result in delineation of areas which are larger than the territories held by individuals at any particular time, since territory size might change seasonally (Moran and Sale 1977) and boundaries will alter with death or movement of neighbours (Sale 1974) or changing environmental factors such as tidal movements or currents (Potts 1973).

The use an individual makes of its territory is rarely, if ever, evenly spread throughout the area. Gronell (1980) notes that "it more often consists of a number of separate areas of varying importance, linked to each other by paths", paths being routes used to move between one part of the territory and another. Space use by fish within territories can be mapped in more detail if the territory is

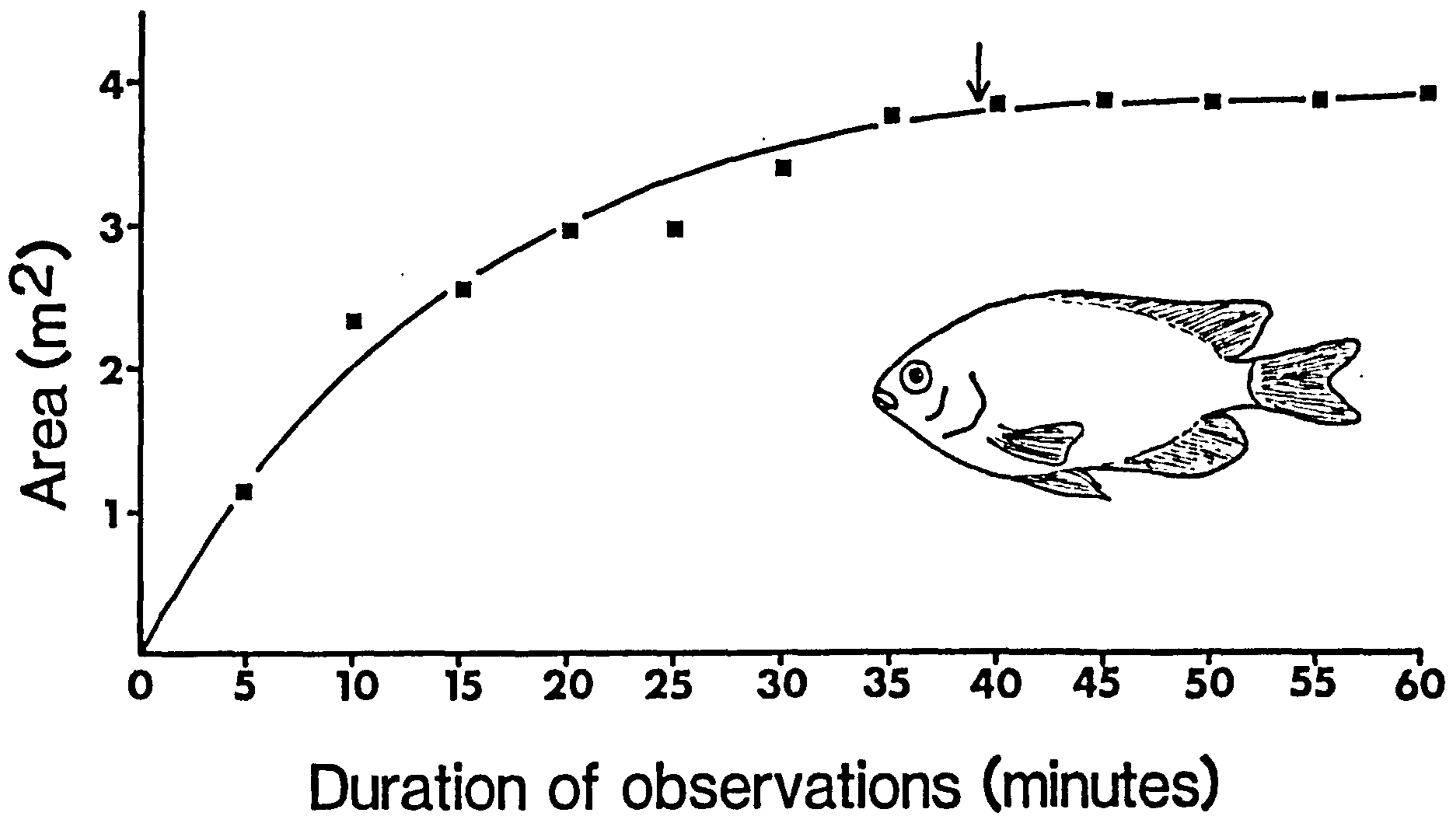


Figure 1: Time-area curve for an individual of the damselfish Pomacentrus flavicauda at One Tree Island, Great Barrier Reef. The arrow indicates the point after which continued observations result in only a 5% increase in the apparent territory size of the fish. This represents the minimum observation period.

subdivided into smaller units. Nursall (1981) and Hixon (1981) have done this directly in the field. Nursall placed a 1m² grid consisting of sixteen subsquares, over a territory of the blenny Ophioblennius atlanticus and recorded the frequency of use of each square by the subject. Hixon, studying a larger fish, the surfperch Embiotoca jacksoni, established 1m² grid patterns over territories using plastic surveying tape attached to the substratum to mark the corners of each quadrat and monitored use of each in a similar manner. Gronell (1980) and Larson (1980) mapped territories first and then superimposed grids over the maps. Larson notes that the amount of time spent in areas frequently used by the fish was underestimated and in infrequently used areas overestimated using this technique. This is because a fish was only recorded twice in a square if it left and subsequently reentered it. Hence, if a fish spends a lot of time in a square without leaving it, for example one containing a refuge hole, then use of that square will be underestimated. The method of mapping used by Gronell (1980), that of marking the location of the subject every fifteen seconds, is less sensitive to this form of error. Figure 2 illustrates the different stages in plotting territories of a colony of herbivorous damselfish.

In some species of fish, territories can be distinguished directly by the effect of the fish's activities on the substratum. This is particularly so amongst herbivorous species such as surgeonfish and damselfish. Montgomery (1980) distinguished territories of the damselfish Microspathodon dorsalis on the basis of their containing a near monoculture of the red alga Polysiphonia sp.. This contrasted strongly with the thicker, mixed species mat outside territories. Where the subject of the investigation is not the fish itself but the substratum within the territory, territories have often been distinguished in this way (e.g. Lassuy 1980; Lobel 1980) or have simply been inferred from the locations of the fish (Hixon and Brostoff 1983).

Problems in mapping territories

One of the main problems of mapping territories by following the movements of the subject rather than by plotting the locations of aggressive interactions, is that it is assumed that the movements lie

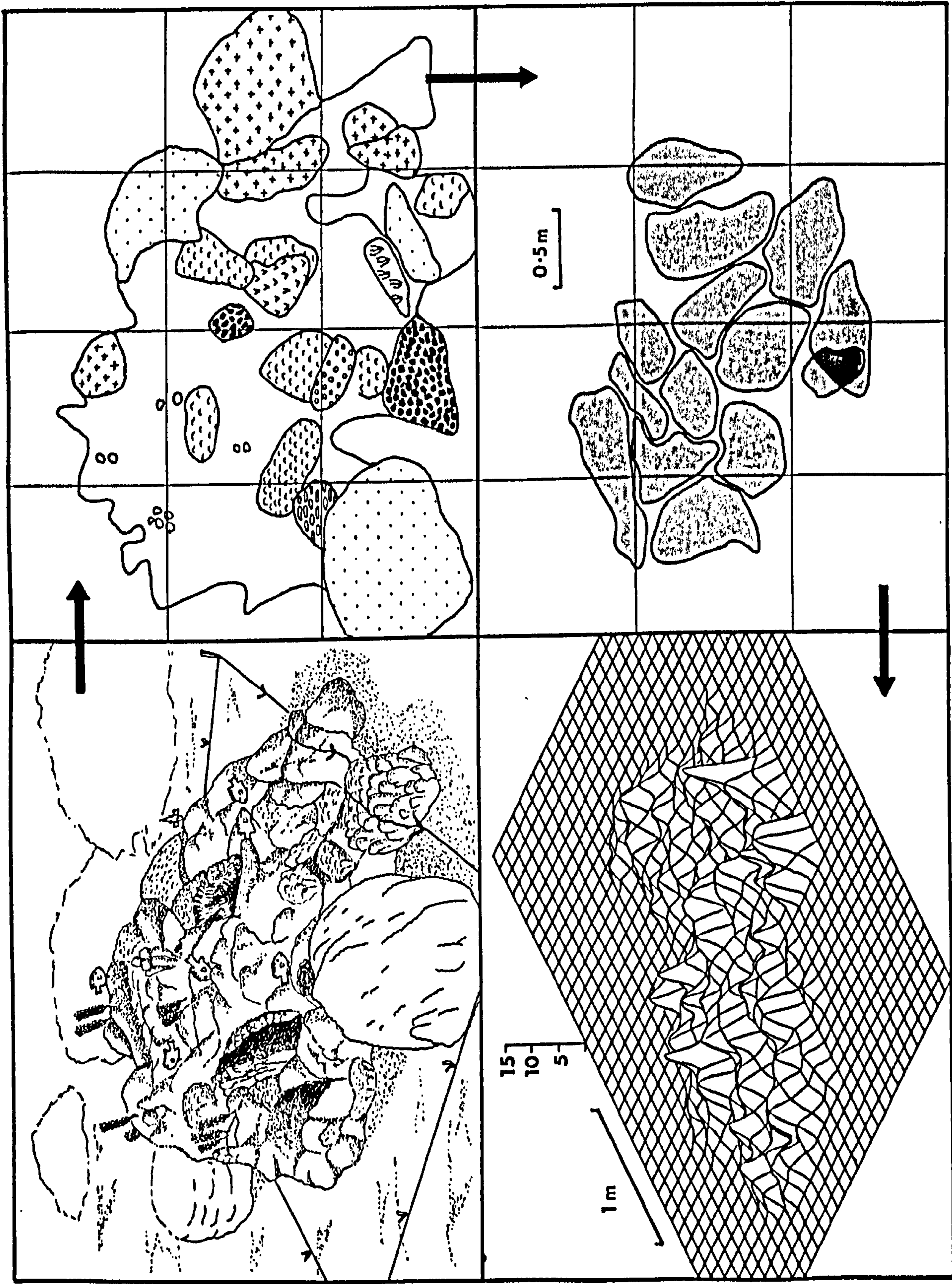


Figure 2: Stages in plotting territories. (a) Patch reef inhabited by a colony of the damselfish *Stegastes nigricans* at Moorea, French Polynesia. The area has been marked out with polypropylene ropes. (b) Sketch map of patch reef prepared prior to plotting territories. (c) Map of territories. Each individual was observed for twenty minutes and its location recorded at ten second intervals. (d) Three-dimensional map of space use by fish within the colony. The map was divided into 10 x 10cm grid squares subsequent to observations. Heights of peaks represent frequency of observation of fish within each square.

within the bounds of the territory. This is not always the case. I have already mentioned that chases may become extra-territorial where territories are contiguous but movements outside the territory occur for other reasons. Clustering is a common phenomenon amongst territorial fish, the significance of which is not fully understood (Reese 1975; Moyer 1980; Thresher 1980). Typically, two or more individuals leave their territories for short periods (up to several minutes long) and "congregate at a single point and mill about while engaged in low intensity agonistic and occasionally courtship displays" (Thresher 1980). Cluster participants often adopt a colouration different from the normal and swimming behaviour may be atypical (Thresher 1980).

Whilst many fish possess refuge holes within their territories (Low 1971; Moran and Sale 1977) others may leave the territory at the approach of a predator. Vine (1974) describes how groups of the surgeonfish Acanthurus sohal periodically 'stampede' off their territories into deeper water, usually at the approach of a predator. Although normally feeding within the bounds of their territories, this herbivorous species will also occasionally form large groups which move across the reef swamping the defences of other territorial fish (often of the same species), feeding freely for a time before moving on (Vine 1974; personal observations). Individuals of A. sohal will also readily move off their territories without any obvious external stimulus. Territories of fish usually have a pronounced vertical component (Thresher 1978). By moving up in the water column to a height of 1.5m to 2m above the substratum, an individual may move freely over the territories of other A. sohal without eliciting aggression (personal observations).

Bartels (1984) describes another form of extra-territorial movement in the damselfish Stegastes dorsopunicans (= Eupomacentrus dorsopunicans). These may leave their territories for short periods, moving distances of up to 16m away. The movements seem to be associated with a search for better sites in which to establish territories. As juveniles, many species of fish settle into sites within the territories of adults (Ross 1978; Fricke 1980; Sale et al. 1980; Pressley 1981). Initially, they may be difficult for the adult to exclude because they use the topography of the territory to escape from adult aggression (Sale et al. 1980) or they may not be excluded

because their colouration reduces aggression towards them by adults (Thresher 1978; Fricke 1980). As they grow they will either be able to better establish themselves and enlarge their territories or be forced to leave by the adults and so must search for new sites. Adults and juveniles holding territories in areas of sub-optimal habitat may also seek new sites for territory establishment.

A further form of extra-territorial movement is less frequent than those already discussed. Females usually leave the territory to spawn. Males also occasionally leave territories to mate. When mapping territories, the best way to respond to extra-territorial movements is to stop the clock (if observations are being timed) and wait for the subject to return. Excursions are usually short and unless very frequent will cause little difficulty.

A second problem in mapping territories is that of being sure that the individuals under observation are exhibiting territorial behaviour. Under some conditions, fish of a normally territorial species abandon territoriality. Doherty (1982) built artificial patch reefs in the lagoon of One Tree Reef, Great Barrier Reef, and stocked these with juveniles of two species of territorial damselfish at different densities. On some of the reefs he noted that rather than holding territories, Pomacentrus wardi appeared to be organised into dominance hierarchies. I have observed this in the Red Sea where the damselfish Chrysiptera unimaculata may be either territorial or forms dominance hierarchies, the home ranges of individuals overlapping extensively. This appears to be linked to the abundance of food and the availability of shelter. In areas where food (filamentous algae) is abundant and shelter holes are limited, dominance hierarchies appear to be formed. In contrast, in areas where shelter is readily available and algal standing crop lower, individuals hold territories (Roberts, unpublished data). Clarke (1970) noted a similar relationship in the damselfish Hypsypops rubicunda. At one site, none of the individuals of this normally territorial species held territories. In this area there were only two shelter holes and these were used communally.

It will become obvious over only a short period of observations if the fish under study are holding territories or not.

Reese (1975), in his study of butterflyfish, notes several further problems in studies of territoriality and social behaviour. In

areas where visibility was poor or which were spearfished, the fish were wary and would not allow close approach by an observer. These factors should be borne in mind when selecting the study site. The weather can also be a problem. In the same study, Reese found that on rough days there was less feeding and no social interactions between neighbouring fish were observed.

TIME BUDGET STUDIES

More detailed information on the nature and function of territoriality can be obtained by using a time-budgeting approach (Hixon, personal communication). Time-budgets have been measured in several ways and these methods can be divided into two categories: studies in which continuous recordings of activities have been made and those in which activities are recorded at intervals. A characteristic of both these approaches is that only a limited number of behaviours are distinguished to simplify the recording procedure.

Nursall (1981) recorded six activities in his study of Ophioblennius atlanticus. The activity which an individual was engaged in was recorded every few seconds over observation periods of varying length. Timing the intervals between recordings was a problem. After experimenting with flashing or ticking metronomic devices but finding that they had very short sea-lives, Nursall settled on estimation of the interval, noting "I tried to establish rhythmic repetition of code entry by singing repetitious measures silently to myself as I worked". This method of timing has the advantage that the observer can fix attention on the subject without having to keep looking at a stopwatch or other timing device, an important advantage when observing fast moving or cryptically coloured species. Alternatively, intervals may be estimated by counting seconds silently.

A problem with making recordings at intervals is that a proportion of activities will be missed. A sequence of several activities may take only a few seconds and hence some will not be recorded. Nursall (1981) notes that if recordings are made sufficiently regularly and rapidly then the statistical pattern of activity will emerge.

A second form of interval recording of time-budgets involves the recording of event frequency data. Each activity distinguished is

recorded as a single event each time it occurs. This reduces the problem of missed activities since these will only be missed during particularly rapid sequences of activities, whilst writing down events (if not using a tape recorder or event recorder) and when the subject is temporarily obscured by some topographic feature of the study site or by other fish. Warner and Hoffman (1980) have used this approach. Hixon (personal communication), studying the damselfish Stegastes fasciolatus, estimated feeding and defence rates of individuals as numbers of feeding bites and aggressive encounters respectively, per unit time.

The disadvantage with event frequency recording is that it assumes that all activities are equal with respect to the time taken on each. Continuous recording of activities overcomes this problem and allows a more accurate representation of the time a fish spends engaged in each type of activity. Each behaviour is simply scored as it occurs and the time spent on it recorded. Clarke (1970), Warner and Hoffman (1980), Jones (1981), and Norman and Jones (1984) have used this approach.

An important consideration when undertaking time-budget studies of behaviour is that there may be diurnal fluctuations or rhythms in levels of activity. To account for this, wherever possible, observations should be evenly distributed throughout the day, the exact time of start and finish of each observation period being recorded. It is important to assess the variability in activity levels if time-budget data are to be used to measure the effect of an experimental manipulation.

If continuous or time interval recordings are being made and the subject is lost from view during observations this should be recorded as such and the period spent out of sight timed like any other activity. As long as the behaviour of the fish does not differ when it is out of view from when it is in view then the results will not be affected.

RECORDING DATA

Activity sequences of fish are often rapid and the problem arises as to how to record them quickly enough. If using a pencil and underwater writing board then it will be impossible to write down all the

activities long-hand. Under such circumstances the use of a mnemonic code is simple and easy to memorise. This approach allows rapid recording of behavioural sequences, makes efficient use of board space and minimises the amount of time which must be spent looking at the board when making notes. It has been used by many (e.g. Reese 1975; Nursall 1981; Thresher and Moyer 1983).

Underwater tape recorders allow continuous recordings of behavioural sequences. Some form of coding should still be used, each behaviour being represented by one or two words. The major advantage of this technique is that the observer need never look away from the subject. Clarke (1971), Reese (1975) and Warner and Hoffman (1980) have used underwater tape recorders. Losey (1978) considered the tape recorder as "probably the single most valuable piece of equipment for the marine ethologist".

An intermediate between these two methods and allowing an even finer level of quantification is the underwater event recorder (Losey 1978). Once proficient in its use, like the underwater tape recorder, attention need never be taken from the subject. Hixon (1981) and Losey (1972) have used event recorders.

For even finer levels of quantification, behavioural sequences can be filmed using either film or video cameras. The advantage of this approach is that rapid or complex sequences of activity can be recorded and subsequently carefully analysed in the laboratory. Reese (1975) used this approach in his study of butterflyfish and Thresher (1976) used a fixed underwater television camera to investigate the territorial behaviour of a damselfish in the absence of a diver. Losey (1978) notes that he has found dramatic changes in the fish community observed on a Hawaiian reef in the presence of a diver and as filmed by a remote television camera. Myrberg (1973) has reviewed the use of underwater television in behavioural studies.

QUANTIFYING AGGRESSIVE BEHAVIOUR

In many studies, interactions between fish have been scored simply as agonistic or non-agonistic (e.g. Low 1971). This gives no indication of the type or intensity of the encounter, information useful when working out the energy expended by a fish in territory defence. Or, it may be desirable to distinguish between the intensity of aggression

shown towards neighbouring territory holders and towards intruders of different species. Such distinction requires a finer level of quantification of agonistic behaviour. In its simplest form this involves subdivision of aggressive responses into broad categories. Roberts (in press) divided aggressive interactions between territory holding individuals and intruders into three categories: (1) display, (2) approach and display, and (3) chase. This avoids the problem of different species having different types of display (although these must first be identified) and has been successfully applied to species from three families of coral reef fish. Sale et al. (1980) used a similar scale for testing the responses of fish to intruders in an experimental set up. Nursall (1974) used a comparable but extended scale distinguishing five levels of reaction intensity in the surgeonfish Acanthurus lineatus: (1) watching, (2) tail chasing, (3) parallel swimming, (4) chasing, and (5) harrying.

For more detailed ethological studies the form of the display is important to define. Rasa (1969) notes that on many occasions, fights between individuals of the damselfish Stegastes fasciolatus (= Pomacentrus jenkinsi) may be won by display alone without contact between the combatants or penetration of either fish's territory by the other. The most common forms of display in fish are summarised below.

(1) Lateral Display - This is probably the most widespread form of teleost display. Typically it involves spreading of the unpaired fins and orientating so that the flank is exposed to the opponent (Figure 3a). The function of this display has frequently been suggested to be to increase the apparent size of the fish although this has been disputed (Zahavi 1981). The functions, forms and evolution of lateral displays are reviewed by Chiszar (1978).

(2) Frontal Display - In this posture the fish faces the opponent with unpaired fins spread and tilts the long axis of the body towards the substratum, head pointing downwards (Zumpe 1965). At this angle the spinous portion of the dorsal fin is directed towards the opponent (Figure 3b).

(3) Circling - The fish chase each other in a tight circle, each apparently trying to bite the caudal regions of the opponent

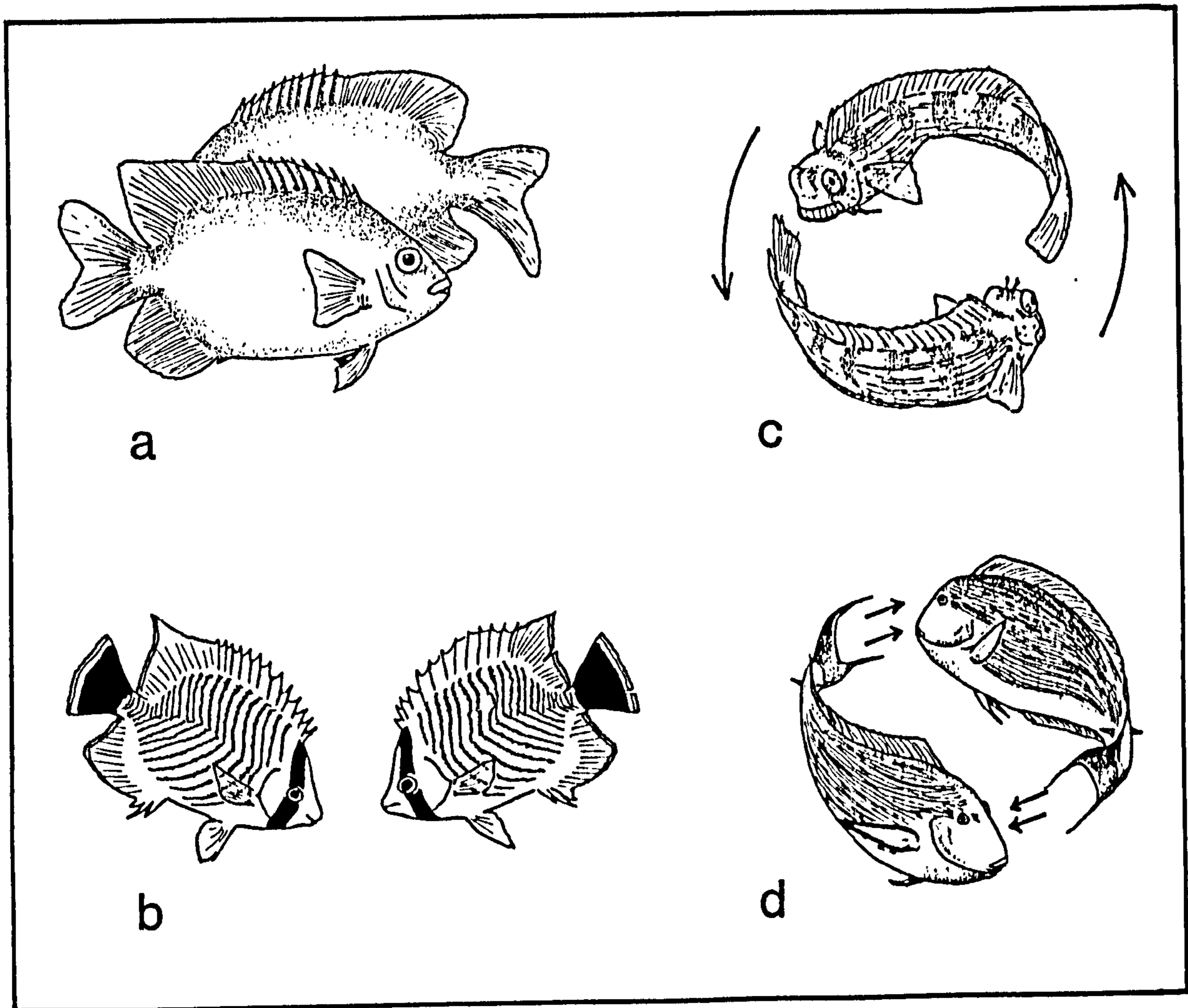


Figure 3: Common forms of fish display. (a) Lateral display in the damselfish *Stegastes nigricans*. (b) Frontal display in the butterflyfish *Chaetodon trifascialis*. (c) Circling in the blenny *Salaria fasciatus*. (d) Tail beating in the surgeonfish *Acanthurus sohal*.

(Zumpe 1965; Rasa 1969; Nursall 1974)(Figure 3c).

(4) Tail Beating - This movement often accompanies a lateral display, the animal beating its tail towards the opponent (Figure 3d). Chiszar (1978) calls this 'water-jetting' and the force of it may be such that one fish may sweep the other away for a short distance (Zumpe 1965; Hamilton and Peterman 1971).

(5) Mouth Gaping - Opponents face each other with mouths wide open (Miller 1978).

(6) Biting - Opponents physically nip or bite each other (Rasa 1969; Nursall 1977).

(7) Jaw Locking - This is where adversaries grab each other's upper or lower jaw. Larson (1980) describes it as the ultimate form of aggression in rockfish (Sebastes spp.).

(8) Pendulum Movements - Opponents face each other, usually at a territory boundary, and alternately move forwards and backwards (Miller 1978; Motta 1983).

(9) Exaggerated Feeding - This is another display typically shown at the territory boundary in which neighbours actively feed, side-by-side, each on their own territory, sometimes following each other for short distances along the boundary (Nursall 1977). It is a common form of display in blennies.

(10) Colour Change - Colour changes frequently accompany other forms of display (Zumpe 1965; Robertson 1983). They may be associated with aggression, appeasement, courtship or other behaviours (Rasa 1969; Thresher 1980; Robertson 1983). Rasa (1969) associated changes in eye colour of the damselfish Stegastes fasciolatus (= Pomacentrus jenkinsi) with intensity of aggression.

There are many other forms of display and the particular displays of the species under study should be recognised through careful preliminary observations before beginning detailed ethological work.

EXPERIMENTAL APPROACHES

Presentation of novel fish to territory holders

Observational studies are useful for formulating hypotheses about the

nature and function of territoriality but to test these hypotheses an experimental approach must be used. A widely used experimental procedure involves the presentation of individuals of the same or different species to the territory holder and assessing the latter's reaction. Such fish may be alive, dead or modelled from various materials. This approach has been used to investigate many aspects of territoriality including territory size, range of species excluded, effects of size of intruders on intensity of aggressive response of the territory holder, individual recognition, effects of colouration and the nature of aggression.

The 'model-bottle' technique This has been the most widely used method of introducing novel fish to territory holders and was developed by Myrberg and Thresher (1974). A fish is enclosed within a glass jar, or occasionally a polythene bag (Ross 1978; Brockmann 1973), and is presented to the territory holder (Figure 4). To measure territory size the container with the fish is first placed at some point outside the territory. The territory holder generally moves in the direction of the container, stops before reaching it, and then resumes other activities. A period of thirty seconds is then allowed before the observer moves the container closer to the territory. This procedure is repeated until the territory holder attacks the 'intruder' by nipping or butting the container. The distance is then measured from the reference point (usually the focal point of the territory). The procedure is repeated several times and the average distance from the residence taken as the 'maximum distance of attack', an estimate of territory size (Myrberg and Thresher 1974). Using this technique Myrberg and Thresher found that different species were responded to at different distances by individuals of the damselfish Stegastes planifrons (= Eupomacentrus planifrons), and they termed this the serial territory. The same effect has been found in several subsequent studies in which the model-bottle technique has been used (Thresher 1976, 1978; Moran and Sale 1977; Mahoney 1981). This approach to measuring territory size has been applied primarily to measurement of non-contiguous territories because of the confounding effects of neighbouring territory holders on the responses of the subject.

Myrberg and Thresher (1974) also devised a method of quantifying

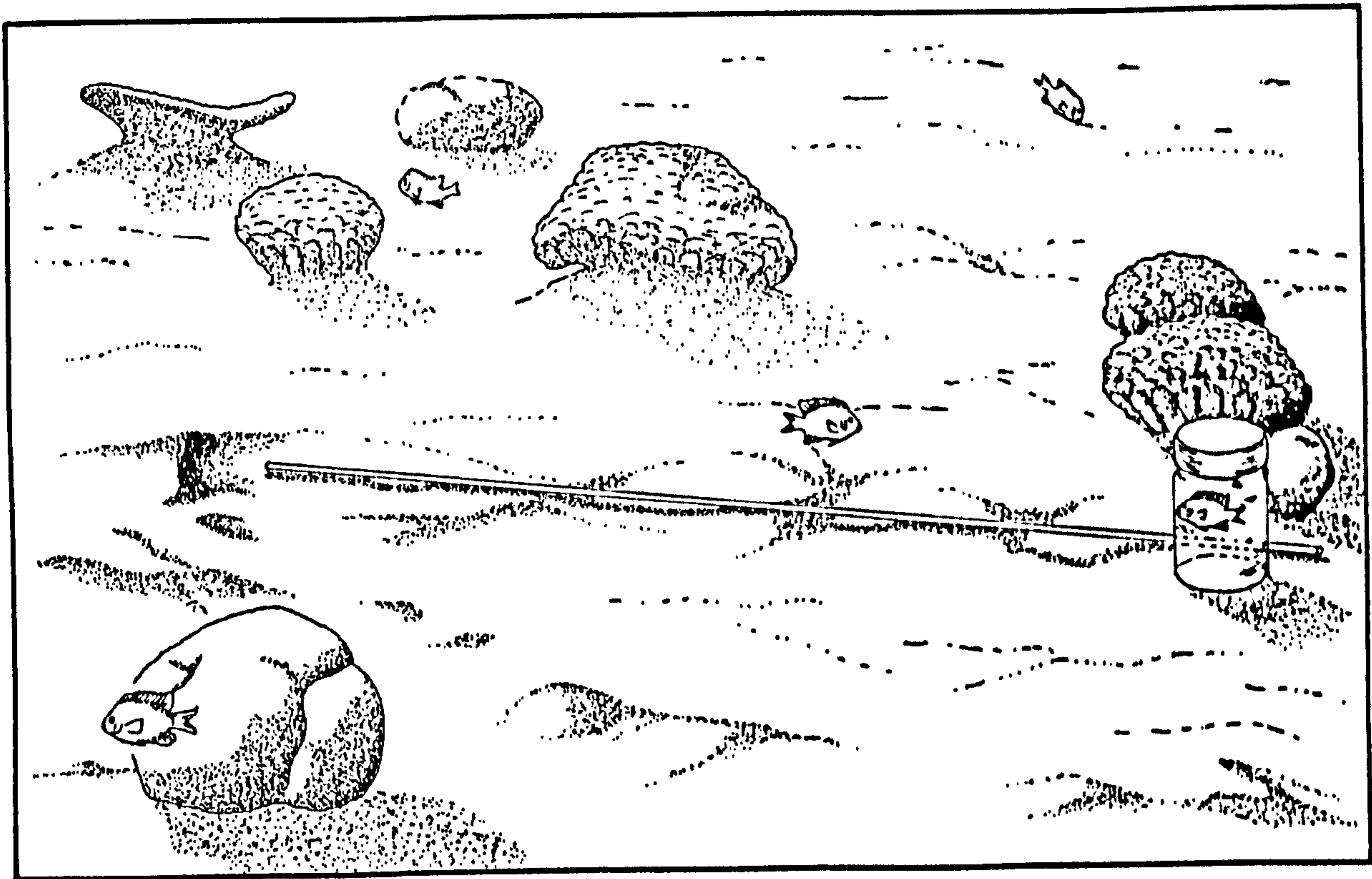


Figure 4: The model-bottle technique of measuring territory size. The 'intruder' is enclosed within a jar and presented to a free-living, territorial fish. Maximum distance of attack is measured along a graduated rod placed on the substratum using a refuge hole as the reference point.

the intensity of aggression displayed towards 'intruders'. They placed the bottle with captive fish in the centre of the territory, next to the 'residence', and counted the number of times the resident nipped or butted the jar within a period of three minutes. Thresher (1978) found that the attack rate was not constant with time since presentation, attack rate initially increasing and then declining depending on the distance from the 'residence'. He used the number of attacks over a shorter period, one minute, as a measure of aggressive intensity.

The model-bottle technique has also been used by Sale et al. (1980) to test the responses of resident adult damselfish to 'intruding' juveniles, by Moyer (1980) to test the responses by anemonefish of each sex to 'intruders' of different sexes, by Ross (1978) to assess the effect of size of 'intruder' on intensity of territorial defence in anemonefish, and by Thresher (1979) to investigate whether territorial damselfish are able to recognise each other as individuals.

The problems associated with the model-bottle technique are such that some feel that the results obtained using it are artifacts of the method. The objections to this technique are as follows:

(1) The fish contained within the bottle appears to act as a supernormal stimulus. This seems to be partly because it is unable to flee and partly because the fish within the bottle is stressed by the confinement and inability to flee from attackers. Donaldson (personal communication) notes that 'model' damselfish, Stegastes albifasciatus, often lost colour, gave frequent threat displays and repeatedly tried to escape from the bottle. He notes that territory defenders would attack the 'model' fish well beyond the territory boundaries in response to such stress-related displays. Hixon (personal communication) notes that territory occupants appear to spend a disproportionate amount of time attacking the model-bottle. To try to reduce stress-related behaviour in their 'model' fish, Myrberg and Thresher (1974) left them within jars for thirty minutes before presentation to territory holders. This may reduce stress but it will not remove it and the degree to which each fish is stressed will vary between species and between individuals of a species.

It will also vary depending on the method of capture.

(2) The position of the 'model' may be difficult to control in shallow water with even slight wave action. This is particularly a problem if 'models' are enclosed within plastic bags. Donaldson (1981) tried to investigate the effects of height above the substratum of 'model' fish on the attack rates and maximum distance of attack by territory holding Stegastes albifasciatus. He found great difficulty in controlling the positions of 'models'.

(3) Control stimuli (water filled bottles or plastic bags) are sometimes attacked (e.g. Ross 1978; Donaldson, personal communication). This may be partially due to the sequence of presentation of 'models' and controls. If controls are presented subsequent to 'models' then territory holders might have learned to associate containers with intruders and the containers themselves will elicit attacks.

(4) The reference point from which the maximum distance of attack is commonly measured, the 'residence' (refuge hole or nest), rarely lies centrally in the territory. Sometimes also, more than one refuge hole is used by the fish (personal observations). Measurements of territory size using the model-bottle technique are thus sensitive to the direction from which the bottle is presented. Part of the seasonal variation in territory size of the damselfish Parma microlepis, found by Moran and Sale (1977) may have been due to differences in direction of presentation since this was not fixed. To overcome this problem a large number of presentations should be made from many different directions and the maximum distance of attack averaged.

The serial territory has only been clearly demonstrated using the model-bottle technique. Thresher (1976) found suggestive but weak evidence for discrimination between species in the distances from the territory centre at which they were attacked from video film taken using a remote camera directed at a territory of the damselfish Stegastes planifrons (= Eupomacentrus planifrons). Robertson et al. (1979) describe individuals of the surgeonfish Acanthurus lineatus as "attacking members of other species, and especially feeding schools of Acanthurus triostegus, further outside territories than they attacked

conspecifics". However, this could simply be due to habituation of aggressive responses to neighbouring territory holding conspecifics which must come closer to intrusion into the territory before eliciting aggression. It is perhaps not surprising that the serial territory is difficult to demonstrate from observations of natural intrusions. Thresher (1978) identifies sources of variation in the distance from the residence at which an intruder is attacked which may mask any discrimination between species by the resident as evidenced by maximum distance of attack. The height above the substratum, speed, and direction of entry into the territory will all have an effect on where the intruder is when it first elicits an attack from the territory holder. Furthermore, the intruder may be obscured from the resident by some topographic feature so that it is not noticed until it is well within the territory. Moran and Sale (1977) studied serial territoriality and argued that the serial territory concept was unnecessarily complex suggesting that it is an artifact of the model-bottle technique. They interpreted differences in maximum distance of attack toward different species of 'intruder' as simply reflecting greater or lesser tendencies on the part of the territory holder to attack these species. These differences in motivation to attack are expressed as a willingness to move further from shelter to attack some species than others.

Hixon (personal communication) suggests that the model-bottle technique be abandoned as a method of measuring territory size because of these many problems whilst accepting its use for other purposes, noting that it has been used successfully to increase territory defence costs in butterflyfish (T. Tricas, unpublished data). It also appears to be a useful method for assessing whether fish can recognise each other as individuals (Thresher 1979).

Models of fish Experiments which involve the introduction of novel fish to territory holders have also been performed using model fish made from dead specimens or other materials. This approach can be usefully used to investigate the effects of size, shape and colour pattern of the test 'fish' on subjects holding territories (Tinbergen 1948; Potts 1973).

Helfman (1983) has described a method for using dead fish as models. Weights or foam are packed into the ventrum of a freshly

killed specimen depending on whether a positively or negatively buoyant model is required. The body cavity is filled with silicon cement to preserve the shape. The specimen is then preserved in formalin through injection and overnight immersion, wiped dry with paper towelling and a moderately thick layer of fibreglass resin/catalyst mixture applied. Further coats may be added. The model can then be painted to restore 'natural' colouration. Helfman indicates that the best results using these models were obtained when they were presented to fish attached to the end of a clear perspex rod held by a diver. Buoyant models can be tethered to the bottom using monofilament fishing line. Rasa (1971) used dried and painted specimens in her aquarium studies of the damselfish Microspathodon chrysurus. However, the drying process causes shrinkage and other deformations. Helfman's technique overcomes this problem.

Brockmann (1973) used live and dead painted fish confined within plastic bags to investigate the role of poster colouration and other cues, such as shape and size, on the territorial behaviour of Stegastes leucosticus (= Eupomacentrus leucosticus). Live 'models' were prepared by capturing and anaesthetising a fish, blotting it dry and painting it with acrylic paint. The fish was then revived in a bucket of seawater and placed into a plastic bag filled with seawater for the trial. The whole procedure lasted between ten and fifteen minutes. Brockmann notes that differences in age, sex, maturity and the presence of a nest or eggs as well as previous experience and learning can all influence the responses of a fish to a model and hence made the results of trials difficult to interpret. In addition, when the response of a fish to a model was low then differences between models were difficult to detect.

Ehrlich et al. (1977), in their study of social behaviour in butterflyfish, used models of different species cut out of plywood and painted realistically, being presented to fish at the end of 60cm, clear perspex rods. Both painted and blank sides of the model were presented and the fish's responses to each noted. Fricke (1980) also used painted plywood models to investigate the responses of adult angelfish (Pomacanthus imperator) to juvenile and adult coloured fish. The models were floated from short monofilament lines attached to weights buried in sand on the substratum. He found that the models seemed to alarm subject fish and so each test was ended at the first

clear flight reaction of the subject. Successive presentations at intervals of three minutes gave very inconsistent results and so a large number of replicates were necessary.

Kohda (1981) in a laboratory based study of aggression in the damselfish Stegastes altus (= Eupomacentrus altus), used models cut from 3mm thick sheets of plastic. Using these he investigated the effects of size, shape and colouration on the aggressive responses of subject fish. This approach could be extended to field studies using the methods of presentation outlined above.

Despite their artificiality the above techniques offer a means by which investigators may study the cues through which fish recognise competitors and the stimuli which 'release' aggression. It is very difficult to assess the effect of size, shape and colouration using live fish because of the difficulty of holding other factors constant whilst varying one. For example, Fricke (1973) concluded that individuals from a monogamous pair of the damselfish Amphiprion bicinctus recognised each other by their colouration after individuals which had been dyed elicited aggressive responses from their partners. However, this may have been a reaction to the new colouration and not aggression caused by failure to recognise the fish.

Manipulation of resources

A manipulative approach has frequently been used in investigations of the adaptive significance of territoriality, the levels of particular resources within territories being altered. (A typical approach is to increase the availability of a resource in some territories, decrease its availability in others and leave some territories unmanipulated as controls.) The most frequently manipulated resource has been the abundance of food. The consequences of altering levels of food within territories have been studied by Ebersole (1980), Hixon (1981) and Norman and Jones (1984). Ebersole (1980) mapped territories of the damselfish Stegastes leucosticus (= Eupomacentrus leucosticus) before manipulation, then added food (algal laden coral fragments) in a grid pattern both inside and outside the territories under study. The territories used were non-contiguous, eliminating the effects of neighbouring territorial damselfish on any expansion or contraction of territories as a result of the manipulation. Territories were then

remapped two days later.

In a similar experiment, Norman and Jones (1984) manipulated food abundance in territories of another damselfish, Parma victoriae. Food was added by transplanting algal covered rocks to areas of bare rock and sand which were a characteristic of most territories. Food was removed by scraping algae from a number of quadrats spread throughout the territory. Food manipulations will not necessarily influence territory size when borders are constrained by intraspecific interactions (Ewald and Carpenter 1978) or topographic features. Norman and Jones assessed the effects of neighbouring territory holding conspecifics by removing them from areas surrounding territories subjected to different treatments. Hixon (1981) manipulated food abundance in territories of the surfperch, Embiotoca jacksoni, reducing food abundance by covering areas of the territory with netting anchored by bricks. Food abundance was increased by bringing rocks from the territories of another fish species into unproductive areas of E. jacksoni territories. These rocks were rich in tube-dwelling amphipods, the primary prey of E. jacksoni.

Whilst Ebersole (1980) measured only territory size before and after treatments, Hixon (1981) and Norman and Jones (1984) also measured time-budgets of the study fish. Hixon (personal communication) notes that since only three responses in territory size are possible after a manipulation, increase, decrease or no change, agreement between observations and a model could be purely fortuitous. He believes that detailed time-budget studies are the best tool for studying territorial behaviour and that predictions about how time-budgets should change under different conditions should be incorporated into models of territory size.

Norman and Jones (1984) identify further weaknesses of studies using food manipulations: (1) failure to distribute resources in a realistic manner, (2) using sample sizes too small for statistical analysis, and (3) failure to control for temporal changes in territory size. Hixon (1981) distributed resources in a rather clumped manner, introducing regions of high food density into territories. He measured territory size one hour, two days and eight days after the manipulation. It is to be expected that the apparent size of the territory will be smaller shortly after such a food manipulation, occupants feeding intensively in small areas and perhaps thus allowing

intruders to penetrate further into the territory before responding. If Hixon had not measured territory size by plotting the locations of aggressive encounters but instead mapped the movements of the fish, as did Ebersole (1980), the apparent decrease in territory size may have been even greater. Territories supplemented with food may also contract due to increased intruder pressure (Hixon 1981). Ideally, food abundance should be increased or decreased evenly throughout the territory area (if food is normally evenly distributed within the territory). This is rarely possible under field conditions. Hixon (personal communication) has induced damselfish to establish territories on flat, artificial substrate modules. With these, more accurate and even manipulations of food abundance are possible.

Manipulating resources other than food is often less easy. Hixon (1981) altered the numbers of shelter holes in E. jacksoni territories but the man-made crevices were unsuitable for the fish and the results inconclusive.

Nursall (1981) observed that the blenny O. atlanticus spends most of its time feeding in a small part of its territory and concluded that territories provided more than the minimal needs of the fish. Nursall criticises the assertion that territory sizes are normally optimal and suggests that actual space utilisation probably slides around some optimum. The question of whether optimality of territory sizes exists in reality and if it does whether fish are able to adjust territory size to approximate an optimum must be investigated manipulatively. Up to now there have been few really satisfactory tests of these questions using food manipulations.

Manipulation of fish population densities

Experiments involving manipulations of the population densities of fish are generally designed to assess the impact of competitors (for food, space, matings etc.) on the territory sizes of subject fish, or, whether fish of one species are affecting the distribution of one or more other species. Removals are generally effected by spearing fish but may employ anaesthetics such as quinaldine, whilst additions are usually of fish captured using anaesthetics or nets. In their simplest form manipulative experiments of this type involve removal of neighbouring fish, usually conspecifics, holding contiguous

territories and monitoring any consequent changes in the territory size of the subject. Norman and Jones (1984) used this approach, combining it with food density manipulations in a factorial experiment to assess the effect of neighbouring territory holders on size changes of territories as a result of food manipulations. Nursall (1977), in a more limited experiment, removed five territory holding blennies, each from a different area, and monitored changes in the territory sizes of neighbouring individuals. He found a rapid expansion of neighbouring territories, with a suggestion that fish with small territories were the first to respond to the removal.

Low (1971) monitored intrusion rates by other species of fish into territory areas of the damselfish Pomacentrus flavicauda before and after territory holders were removed. Thompson and Jones (1983) removed all the blennies (Fosterygion varium) from two 25m² areas to assess their influence on the feeding rates of the wrasse Pseudolabrus celidotus within these areas. They note however, that although such experiments often show that removal of one species results in a local change in the distribution of another, this does not on its own demonstrate competition between these species. This is because they do not establish that one species has a deleterious effect on the other. An effect of one species on where another forages is not necessarily detrimental but if that species affects the quantity of food taken by the other then the effect is harmful.

There have been many other uses of removal experiments. For example Clarke (1970) used a removal experiment to study repopulation of sites by the damselfish Hypsypops rubicunda. Hixon (1981) removed territory holding E. jacksoni to assess the rapidity with which they were replaced. Pressley (1981) used removals to study pair formation in the bass Serranus tigrinus which hold territories as pairs. Robertson and Polunin (1981) removed territorial damselfish to assess competitive dominance through patterns of replacement and Sale (1976) has used removal experiments to investigate the influence of adult damselfish on juvenile recruitment and survival.

Hixon (personal communication) manipulated the densities of food competitors (small parrotfish) of the damselfish Stegastes fasciolatus to assess the effect of competitor density on damselfish territory size. This was achieved by constructing 25m² enclosures in situ around existing territories. Parrotfish were added to these enclosures at

varying densities and the time-budgets and territory sizes of the damselfish were measured. Terminal phase Thalassoma bifasciatum hold mating territories. Warner and Hoffman (1980) used patch reefs as natural enclosures, manipulating densities and sex ratios of initial phase wrasse to assess their effect on defence costs and breeding success of territory holding males.

Additions of territory holding fishes are usually more difficult to perform due to rapid movement from areas to which they are added or low post-addition survival. Nursall (1977) added ten marked blennies to areas of established blenny territories. These quickly left the site of release. Only one was observed to be successful in establishing a territory and this was discovered by chance 54m from the site at which it was initially released. Sale (1976) found that survival of juvenile damselfish added to rubble patches was poor whether or not they were added to undisturbed patches or to patches from which adults had been removed, even though they were added at sunset in an attempt to maximise the number which remained at the site of release (since added fish were diurnal). Doherty (1982) built artificial lagoonal patch reefs and introduced damselfish juveniles to them at various densities and species combinations in an experiment to test the effect of population density on juvenile growth and survival. In an attempt to overcome the problem of post-addition losses from these reefs he continued adding fish over a period of seven days until the desired treatments had been approximated and had remained stable for approximately three days.

Addition and removal experiments have provided very useful insights into the social and community structures of territorial fish and often provide the only effective tests of hypotheses concerning the functions of territorial behaviour. However, they are difficult to perform, particularly in the case of addition experiments where post-addition losses can be high. Removals can also be difficult, especially of very mobile or timid species. Nursall (1981) found that blennies, if not caught on the first two or three shots with a spear, were virtually impossible to capture and would no longer tolerate an observer. In areas which are regularly spearfished, fish are often very wary and consequently difficult to capture. Under these circumstances alternative sites should be chosen.

Problems of stress in manipulation and human interference on fish behaviour

One of the most serious causes of stress to fish is from capture and handling. If fish must be captured for the purposes of experimentation then time spent in captivity must be minimised. Ideally, the method of capture should also be non-damaging. This is particularly important where fish must be repeatedly recaptured, as for example in studies requiring measurement of growth rates. For small territorial fish, capture using large plastic bags meets these criteria. A fish can be driven into a plastic bag placed at a strategic point in the territory, or, if the fish is carnivorous, the bag can be baited and the fish allowed to enter at will. This method of capture involves little trauma to the fish as evidenced by multiple recaptures of pseudochromids using baited bags (D.J. Ferrell, personal communication).

A second important source of stress to fish arises simply from the presence of the observer. To a fish, the diver probably appears as a large, noisy, potential predator (Chapman, in press). Different species of fish react to divers in different ways. Large territorial fish may leave their territories at the approach of a diver whilst smaller fish will rarely do so. However, they may spend more time hidden within refuges in the territory than when the diver is absent. The presence of the diver can also affect use of space by the subject fish. Figure 5a shows how a diver positioned too close to the subject can alter its use of space within the territory. Diver presence may also affect the behaviour of the fish indirectly by influencing its interactions with other fish (Figure 5b & c).

A third source of stress to fish results from transplantation to new sites, as in experiments involving density manipulations. Fish added to sites with already established residents may be subject to great stress and may behave abnormally. Additionally, the unfamiliarity of the surroundings could itself cause stress. These problems probably account for the high loss-rate of fish transplanted to new areas.

Experiments involving manipulation of fish densities also suffer from a further problem, that of overcrowding. Such experiments often involve small patch reefs as experimental units and fish are added to

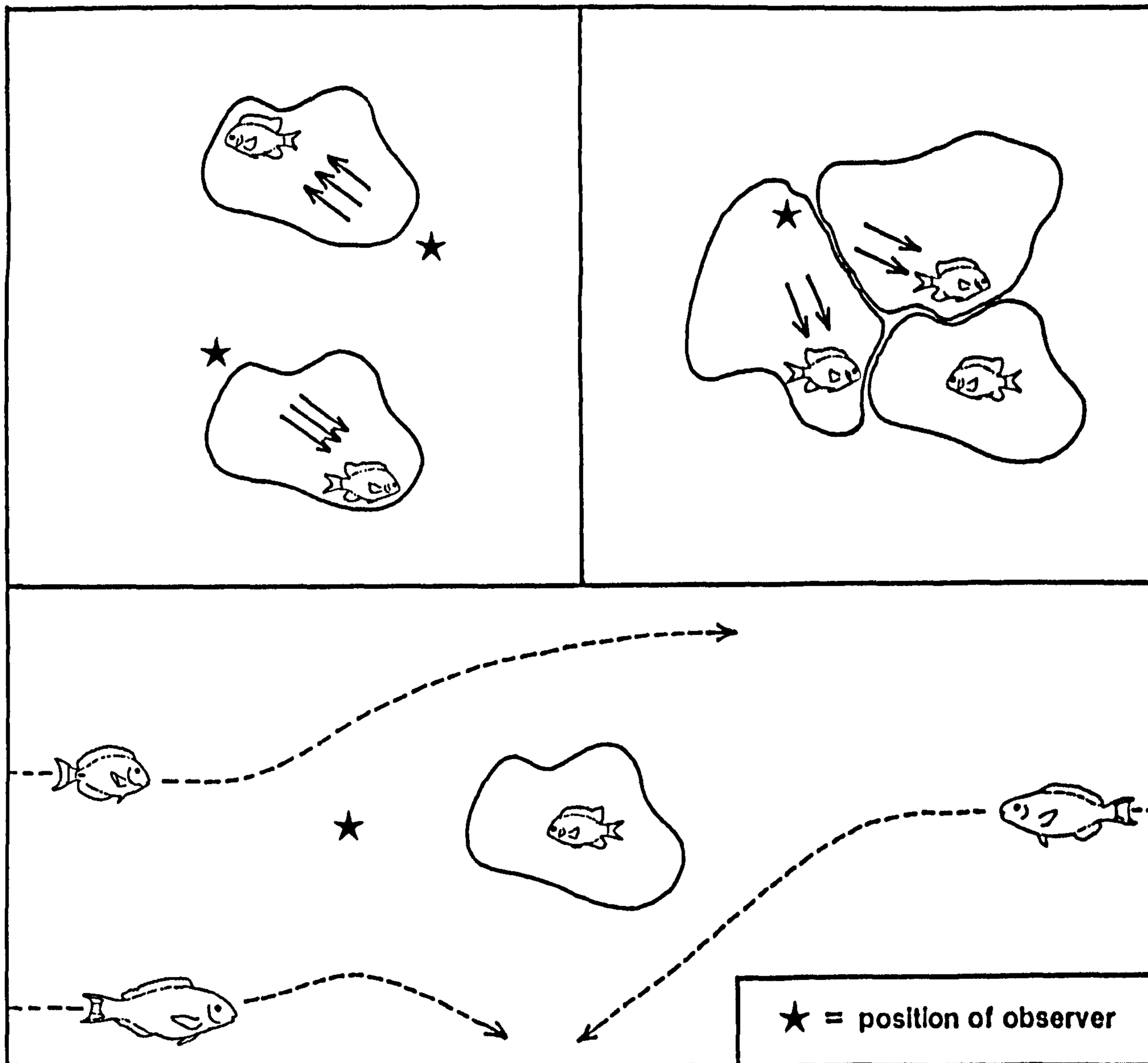


Figure 5: Ways in which the presence of an observer can influence the behaviour of the subject fish. (a) An observer located too close to the subject can cause polarisation of its movements within the territory. (b) Observer positioned within the territories of neighbours of the subject fish can increase the probability of these fish interacting with the subject by forcing them closer to the shared border of the territories. (c) The observer may cause large, mobile fish to alter course. These fish might have interacted with the subject had the observer not been present.

these at varying densities (e.g. Doherty 1982). Fish at high densities are probably subject to considerable stress due to overcrowding, particularly in aggressive species. This possibility should be borne in mind when interpreting the results of experiments where densities of fish are increased.

Density manipulations involving removal of neighbouring territory holders from around the subject fish can also have problems. Removals are often performed using spears and fish learn very quickly the threat posed by spears. The subject fish may subsequently respond to the diver as it would to a predator.

It is important to compare the behaviour of fish under manipulated and unmanipulated conditions in order to assess whether the manipulation has affected their behaviour to the detriment of the experiment.

CONCLUSIONS

Territories can be mapped using many techniques, the most important of which have been outlined in this review. Some, defining the territory as a defended area, feel that mapping should be performed only through marking locations at which territory defence has occurred. This approach is often impractical due to the infrequency of agonistic encounters, particularly between conspecific neighbours of intraspecifically territorial species. This being so, the movements of the resident are mapped, it being assumed that these lie within the bounds of the territory (technically this produces a map of the home-range). The method of mapping used should be chosen according to the aims of the study and the particular territorial system under investigation. It is suggested that the model-bottle technique should not be used for territory measurement primarily because abnormal behaviour of the trapped fish appears to represent a supernormal stimulus to the territory holder. More information about how space within the territory is used is provided by mapping methods which involve the superimposition of a grid over the territory or map of movements of the resident. Measurement of time-budgets of territory holders also provides important information with which hypotheses about the nature and economics of territoriality may be verified.

Observational approaches are most useful in formulation of

hypotheses about territoriality but experimental methods must be used to test these. Experiments are of three main types: (1) the introduction of novel fish to territory holders, (2) manipulation of resources, and (3) addition and removal of potential competitors. The model-bottle technique has been the most widely used method of introducing novel fish to territory holders but suffers from some serious problems which have led to uncertainty as to the validity of the results obtained using it, particularly the finding of serial territories. It does appear to be useful as a means of assessing whether fish can recognise each other as individuals and as a way in which territory defence costs can be increased.

Experiments in which levels of resources have been manipulated have mainly involved altering the availability of food or shelter. The effects of such manipulations have often been difficult to interpret because of (1) failure to control for the effects of population density in the species under study, (2) unrealistic distribution of supplemented or removed resources (mainly food), (3) failure to control for temporal changes in territory size, (4) confounding variables such as increased intruder pressure on territories supplemented with food, (5) using sample sizes too small for statistical analysis, and (6) failure to measure time-budgets of fish before and after manipulations. Future experiments should be designed carefully, bearing these points in mind, in order to minimise ambiguity in the effects of resource manipulations.

Experiments involving addition or removal of potentially competing fish species are primarily used to investigate the functions of territoriality and the effect of one species on the distribution of others. Such manipulations may not be easy to accomplish because of difficulty in capturing individuals to be removed or because of heavy losses of fish from sites to which they have been added through death or movement to other areas. The latter is particularly a problem where experiments are of more than a few days duration. Many experiments which have involved additions or removals have shown an effect of one species on the distribution of one or more other species. Such results should be interpreted cautiously since this does not necessarily mean that the species are competitors. Competition is only demonstrated when the effect of one species on another is shown to be deleterious. No manipulative method is wholly satisfactory but each provides useful

information which should be combined with notes made during extensive observations of the undisturbed and unmanipulated systems.

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